A CONTRIBUTION TO THE HISTOTAXONOMY
OF *CORYLUS* (BETULACEAE)

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INTRODUCTION

The genus *Corylus* has about ten species of trees and shrubs distributed in the temperate regions of the northern hemisphere. The present study concerns the following three species native to Europe : *Corylus avellana* L. = the Common filbert, *C. maxima* Mill. = the Giant filbert and *C. colurna* L. = the Turkish filbert. The first two species have long been under cultivation for their well known edible nuts called filberts or hazelnuts. The last one is occasionally cultivated as an ornamental tree in the parks and along streets. Consequently, there is a considerable literature on the horticulture, biology and the gross-morphological features of the cultivated species and varieties of filberts (BAILEY 1927, EVREINOFF 1958, GOESCHKE 1887, GROSS 1902, HARTWIG 1892, HOWES 1948, KRÜSSMANN 1959, MALLINJAUD 1962, NICHOLSON 1884, OSBORN 1930, REED 1926, RILSTONE 1938, SCHNEIDER 1906, SCHULZ 1892, TURRILL 1956, WEIN 1932, ZIMMERMANN 1922). Relatively speaking, the anatomical and ontogenetic information about the genus *Corylus* is rather scarce being found mainly in the works of ABBE (1935 and 1938), BENSON (1894), HAGERUP (1942), HALL (1952), KIRCHNER, LOEW and SCHRÖTER (1913), METCALFE and CHALK (1950), SOLEREDER (1908).

The present study initiated during the author's survey of literature while searching for anatomical evidences concerning the phylogenetic relationship among the species of *Corylus* as well as among the genera allied with *Corylus*. The terms anatomy and histology are taken as synonyms, and the term histotaxonomy here is used to replace the classical term of "systematic anatomy".

This project was carried out in the following institutions during the author's sabbatical leave granted by Mills College, Oakland, California : Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris; Conservatoire et Jardin Botaniques, Musées de Genève; Botanischer Garten und Institut für Systematische Botanik der Universität Zürich; Royal Botanic Gardens, Kew. I wish to extend my sincere appreciation to the directors of these institutions as well as to their staff members for the generous assistance and cooperation offered during the course of my work. I wish to thank also Professor H. L. MASON,

of the University of California, Berkeley for loaning me the herbarium specimens I needed in this study.

MATERIALS AND TECHNIQUE

The leaf material of *Corylus avellana* which was processed for the study of vasculation of the adult leaf was obtained from anherbarium specimen (U.C. Herb., Berkeley, No. 504321) which was collected by K. KRAUSE (Nº 3843) from the Black Sea coast of Turkey on July 4, 1931. The exact locality as given on the label is : Çukurbük near Samsun, altitude ca. 300 m. above sea level. But the specimen was erroneously named as *Corylus colurna* L. A careful examination of the specimen revealed the fact that the specimen was a typical *C. avellana* L. The juvenile leaf of the *C. avellana* seedling which was obtained from a dried specimen at the Conservatoire Botanique de Genève, was collected by M. MICHELI from Froubenex, on June 23, 1858.

The adult leaf material of *C. maxima* was received from a living specimen in the arboretum of Ecole Dubreuil, Paris. The juvenile leaves of this species were obtained from a dried seedling specimen at the Conservatoire Botanique de Genève, collected by H. ROMIEUX from Florissant, Genève, June 17, 1886. The herbarium sheet of this specimen was erroneously labelled as *C. avellana* but the well preserved nut-shell attached to the seedling was from a typical fruit of *C. maxima* leaving no doubt about the correct identity of the specimen.

The adult leaf material of *C. colurna* was obtained from an herbarium specimen (U.C. Herb., Berkeley, 387846) collected by the REV. JOS. GIRALDI from China interior, Province Schen-si septentr., Kinqua-San, July 10, 1897. The juvenile leaves of this species were collected (KASAPLIGIL Nº 3387) from vigorously growing sucker shoots of a tree at the Jardin des Plantes, Paris.

For the purpose of studying the foliar vasculation, the leaf portions were first discoloured by boiling them in 95 % alcohol. Then, the material was cleared in a 5 % solution of potassium hydroxide within two days at room temperature. Following dehydration through a series of alcohol the material was stained with Safranin O, cleared through a series of xylene and mounted permanently in Canada balsam (cf. FOSTER 1949, Appendix and KASAPLIGIL 1951 a).

Fresh materials for the histological study of the lamina and petiole and the twigs for the study of stem anatomy were collected from living specimens growing in Jardin des Plantes and Arènes de Lutece, Paris. Free hand sections of these materials were fixed and mounted in gelatine glycerine. The maceration of the stem wood for the study of the xylem elements was carried out in an equal amount of mixture of 10 % nitric acid and 10 % chromic acid. The maceration of wood portions took place within 3-4 days at room temperature. The macerated material was thoroughly washed with water using a centrifuge, then dehydrated

through the alcohol series. Part of the macerated wood was stained with Safranin O, and part of it with Iodine green. Safranin staining proved to be more desirable for the microscopic examination. The stained macerated wood elements were processed further through the xylene series by means of a centrifuge and mounted in Canada balsam permanently.

The staminate catkins used in the palynological study were obtained from the following herbarium specimens of the Laboratoire de Phanérogamie in Paris : *Corylus avellana*, Flora Silesiaca, Breslau, Göpperthain, alt. 120 m., collected by C. Baeniz in 1899 ; *C. maxima*, Savi pl. Italia bor., Pisa, collected by Cesati (Nᵒ 750); *C. colurna*, Turkey, Vilayet Kastamoni, Tosya Gavurdagh, collected by Sintenis (Nᵒ 4809) in 1892. The pollen material was bleached with a 3 % solution of KOH and then boiled in glacial acetic acid. Dehydration and staining of the pollen grains were carried out by means of an electric centrifuge, the material then being mounted in glycerine jelly. Pollen material was stained either with a 1 % alcoholic solution of Safranin or with a 1 % alcoholic solution of Methylene blue. Stained material was suitable for the microscopic examination, but for the purpose of photomicrography the slides prepared from unstained pollen grains were more suitable than the ones made from stained pollens.

NOMENCLATURE AND HABIT

1. **Corylus avellana** L., Sp. pl. : 998 (1753) ; A. de Candolle in De Candolle, Prodr. **16** (2) : 130 (1864) ; Tchihatcheff, Asie Min. Bot. **2** : 481 (1866); Boiss., Fl. Or. **4** : 1176 (1879); Beck, Vegetationsverhältn. d. illyrischen Länder (1901); Winkler in Engler, Pflanzenreich **4**, 61 (Heft 19) : 46 (1904); Ascherson and Graebner, Syn. Mitteleur. Fl. **4** : 379 (1910); Hayek, Prodr. Fl. Penins. Balcan. **1** : 69 (1924).

(Synonyms : *Corylus ardua* Poiteau and Turpin. *C. avellana* var. *sylvestris* Aiton, *C. avellana* var. *typica* Schneider, *C. grandis* Dryand. *C. serenyiana* Pluskal, *C. silvestris* Salisbury).

The European filbert is a deciduous shrub, 1-7 m. high. Some rare specimens may exeed 10 m. in height, but always retaining the shrubby habit of many stems and a more or less rounded crown. The basal sprouts grow fast at young stage, but the rate of growth slows down gradually, stems attaining a height of 6-6,5 m. and a diameter of 6-8 cm. in twenty years. The bark of the young twigs is glandular pubescent, reddish brown, becoming smooth and greyish brown by age.

The common varieties of *C. avellana* are : var. *aurea* Kirchn. with yellow leaves; var. *contorta* Bean with curly and twisted twigs; var. *fusco-rubra* Dipp. with purple or reddish leaves; var. *heterophylla* Loud. (Syn. : *C. avellana* var. *laciniata* Döll.) with pinnately dissected leaves; var. *grandis* Ait. with large subglobose nuts. The readers are referred to Geschke's monograph (1887) for the descriptions and classification of cultivated forms and varieties.

2. **Corylus maxima** Miller, Gard. Dict. ed. 8, n° 3 (1768); Spach in Ann. Sc. Nat. Bot. sér. 2, **16** : 106 (1841); Winkler in Engler Pflanzenreich **4**, 61 (Heft 19) : 51 (1904); Hayek, Prodr. Fl. Penins. Balcan. **1** : 69 (1924); Hegi, Ill. Fl. Mitt. Eur. III /1 : 191 (1957); Krüssmann, Handb. Laubgeh. **1** (5) : 351 (1959).

(Synonyms : *C. avellana* var. *Lamberti* (Lodd.) Loudon, *C. avellana* var. *sativa* C. F. Ludwig, *C. avellana* var. *tubulosa* Loudon, *C. avellana* var. *tubulosa alba* (Ait.) Loudon, *C. intermedia* Fingerhut, *C. Lamberti* Lodd., *C. maxima* var. *alba* (Lodd.) Schneider, *C. tubulosa* Willd.).

The Giant filbert is a deciduous shrub, 2-10 m. high. Its habit is quite similar to that of *C. avellana*, but growing more vigorously than the latter. Under favourable conditions, it may attain a height of up to 15 m. Young twigs are reddish brown and covered with glandular hairs. Older stems possess a smooth bark of dark grey-brown colouring.

Corylus maxima var. *atropurpurea* Dochnahl (Syn. *C. avellana purpurea* Loud., *C. avellana atropurpurea, C. atropurpurea, C. atrosanguinea, C. purpurea* Hort., *C. maxima* f. *purpurea* (Loud.) Rehd.) is a very popular ornamental plant with a purple-red foliage and involucre.

3. **Corylus colurna** L., Sp. Pl. : 999 (1753); Tchihatcheff, Asie Min. Bot. **2** : 482 (1866); Boiss. Fl. Or. **4** : 1176 (1879); Winkler in Engler. Pflanzenreich **4**, 61 (Heft 19) : 51 (1904); Hayek, Prodr. Fl. Penins. Balcan. **1** : 69 (1924); Smolianinova in Bull. Appl. Bot. (Pl. Breed.) **21** (5) : 379-449 (1929); Kasapligil, Jour. Calif. Hort. Soc. **24**, 4 : 95-104 (1963).

(Synonyms : *C. arborescens* Münchh., *C. byzantina* Poiteau and Turpin, *C. Jacquemontii* Decaisne).

Unlike the two previous species, the Turkish filbert is a tall tree, usually with a single massive bole. Its height varies from 20 to 40 m. depending on the variety. The stem diameter measures up to 1,25 m. With increased age, the ovate or pyramidal crown shows a tendency to bend towards one direction. Pruning during the young stage of the plant results in a shrubby habit (Kasapligil 1963 a). Young twigs are light yellowish gray and glandular pubescent or setose. Old stems possess a corky, deeply furrowed bark which splits into vertical plate-like segments.

The varieties of the Turkish filbert (*C. colurna* var. *colurna,* var. *glandulifera* A. DC., var. *lacera* (Wall.) A. DC., and var. *chinensis* (Franch.) Burkill) are readily distinguishable through their involucral characteristics (Kasapligil 1963 b).

CLASSIFICATION

The genus *Corylus* was classified under *Coryaceae* by MIRBEL., Elém. Phys. Vég. Bot. **2** : 906 (1815) (cf. REHDER 1949 for further refe-

rences and synonymy). This family was named as *Betulaceae* by AGARDH, Aphor. : 208 (1825) and then also by BARTLING, Ord. Nat. Pl. : 99 (1830). The family *Betulaceae* is divided into two tribes in WINKLER's (1904) monograph : Tribe I : *Coryleae* including *Carpinus, Corylus, Ostrya* and *Ostryopsis* and Tribe II : *Betuleae* including *Betula* and *Alnus*. REHDER (1946) indicates that "the family called *Betulaceae* should bear, according to the rules of priority, the name *Corylaceae*". However, in the 1961 edition of the International Code of Botanical Nomenclature, *Betulaceae* (S.F. Gray, Nat. Arr. Brit. Pl. 2 : 243 (1821) "*Betuloideae*") is listed under *Nomina Familiarum Conservanda* (Appendix II, p. 189 of the Code) with the following note : "If this family is united with *Corylaceae* Mirbel, Elém. Phys. Vég. Bot. 2 : 906 (1815), the name *Betulaceae* must be used".

EICHLER (1875) treats the genus *Corylus* under *Corylaceae* as a separate family from *Betulaceae*, but both belonging to *Amentaceae*. BENTHAM and HOOKER (1862-1883) include both families under *Cupuliferae*. ENGLER and PRANTL (1894), WINKLER (1904), WETTSTEIN (1935) and HEGI (1957) classify the genus *Corylus* under *Betulaceae*, a family of *Fagales*, while the same family occupies an advanced position under *Sapindales* in BESSEY's (1915) system. HUTCHINSON (1959) splits the family into *Betulaceae* comprising *Alnus* and *Betula* in which the staminate flowers possess a calyx, but the pistillate flowers are without perianth, and into *Corylaceae* including *Carpinus, Corylus, Ostrya* and *Ostryopsis*, in which the staminate flowers are without perianth, but pistillate flowers possess a calyx adnate to the ovary resulting an inferior ovary. Actually, these two families of HUTCHINSON correspond to the tribes of *Betuleae* in the classifications of ENGLER and PRANTL (1894) and WINKLER (1904). Should *Betulaceae* and *Corylaceae* merge into a single family as in the Englerian system or should they be separated from each other? Are there histological evidences to justify the separation of *Corylaceae* from *Betulaceae*? The present study was initiated with the hope to shed some light on this problem. I shall return to these questions under the heading "discussion" at the end of this paper.

GEOGRAPHIC DISTRIBUTION

Corylus avellana is distributed throughout Europe from Cintra on the west coast of Portugal, Ireland and Orkney Islands to the southern part of the Ural mountains through Bessarabia, Crimea and Kazakistan. It is abundant throughout the Balkan countries including the coastal regions of eastern Thrace. The northern distribution range extends to 68° northern latitude along the west coast of Norway, to 64° northern latitude in Sweden and 60° northern latitude in Russia along the southern shores of Ladoga lake. In southern Europe it occurs in Spain, Sicily and Greece. It is also recorded from Candia on Crete (M. GANDOGER, May 14, 1915, Herb. Barbey-Boissier, Geneva), but I am not sure about the indigenous nature of this specimen. HOLMBOE (1914) reported its

rare occurrence in the mountain forests of Cyprus. In Asia, it extends from Turkey through Caucasia to Iran in the East and from the Anti-Taurus mountains of Anatolia to Syria and Lebanon in the South. The European filbert is a common shrub in the understory of alder, beech and oak forests. It may form pure stands of its own or be associated with other deciduous shrubs forming thickets in mountain valleys. It is widely cultivated in Turkey, Italy, France, Spain and in other temperate regions of the world.

Corylus maxima is native to south eastern Europe, i.e. Thrace, Macedonia, Croatia and to north eastern Anatolia. This species is recorded from the following localities of Asia Minor: Giresun (KRAUSE 1877), Trabzon (HANDEL—MAZZETTI nos. 71 and 230), Gümüshane (SINTENIS no. 7103). According to KRAUSE (1930) it represents the characteristic plant of the bush forest of the Black Sea coast of Turkey up to an elevation of 1 300 m. where it is also widely cultivated for its nuts. Often it is found naturalized within hedges and orchards in Berlin, Germany and in Steirmark, Austria.

Corylus colurna and its varieties are native to an area extending from south eastern Europe through northern Turkey, Caucasia, northern Iran and the Himalayas to China. Usually, it occurs as scattered trees in deciduous and mixed coniferous forests. The reader is referred to the author's article on this species (KASAPLIGIL 1963 b) for the detail of recorded indigenous localities. However, I would like to list those European localities of cultivated *Corylus colurna* that are known to me, since this species, as compared with the other two, is quite rare in central and western Europe. In the following list the localities of the specimens will be followed by the characteristics of the individuals and references in parenthesies. All measurements and ages that will be cited, are approximate : AUSTRIA: Merkenstein—naturalized in forests (KIRCHNER, O. v. et al. 1913, Lebensgeschichte d. Blütenpflanzen Mitteleuropas **2** : 146-166). — FRANCE: Paris, Pte d'Auteuil, Jardin Fleuriste Municipal —a young tree with branches developing on one side only, 6.5 m. high, d.a.b.h. [1] 7.5 cm., 12 years old (KASAPLIGIL no. 3384 b, Aug. 19, 1962); ibid., Jardin des Plantes, near Laboratoire de Phanérogamie—a healthy tree, 12,5 m. high, with a single bole of 3 m. from ground, d.a.b.h. 30 cm., 25 years old, with fertile fruits, seeds tasty (KASAPLIGIL no. 3386, Aug. 20, 1962); ibid., Rue Buffon, in the courtyard of Chaire Culture—a young tree with ovate crown, 7 m. high, 16 years old, abundant fertile fruits (KASA-PLIGIL no. 3390, Aug. 28, 1962); ibid., Bois de Vincennes, École Dubreuil —the arboretum has the adult trees of two varieties, i.e. var. *chinensis* and var. *glandulifera*, both with fertile nuts (KASAPLIGIL no. 3399 and 3401 respectively, Aug. 31, 1962). — GERMANY: Heidelberg Stiftsmühle —crown elongate-ovate, two stems from ground, height 17 m., d.a.b.h. 58 cm., 60 years old, sterile fruits (Dr. H. HEINE, Paris, personal correspondence, Nov. 6, 1962); vicinity of Mannheim, Neustadt, Hauberan-

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1. D. a. b. h. = diameter at breast's height.

lagen—tree 20 m. high, d.a.b.h. 50-60 cm. (J. WILDE 1936, Kultur-geschichte d. rheinpflanzlichen Baumwelt u. ihrer Naturdenkmale, Verlag Thieme); Thüringen, Bad Köstritz, street plantation—trees with ovate crowns, boles 2.20 m. high, 30-40 years old, fertile fruits (Mitt. d. deutsch. dendr. Ges. 1932); Weteritz, Gardelegen—tree 8 m. high (Mitt. d. deutsch. dendr. Ges. 1934); Lahn, in a garden at Wilhelm Platz—two trees, d.a.b.h. 47 and 56 cm. (Mitt. d. deutsch. dendr. Ges. 1936); Breslau, Scheitniger Park—hardy ornamentals (Mitt. d. deutsch. dendr. Ges. **44** : 531-535, 1932); Bad Reichenhall, Stauffenhof—d.a.b.h. 40 cm., many fertile fruits (Mitt. d. deutsch. dendr. Ges. 1932); Wein-heim near Mannheim, Gräfl. v. Berckheimscher Versuchswald—Trees 56 years old, fruits sterile (F. FABRICIUS 1931, Mitt. d. deutsch. dendr. Ges. **43** : 181-187). — GREAT BRITAIN: Richmond, Surrey, Roy. Bot. Gard., Kew—adult specimens of several varieties (KASAPLIGIL nos. 3420-22, Apr. 22, 1963); Isleworth, Syon House—several tall trees, the tallest 23 m. high, with a clean bole up to 9 m., girth 206 cm. (A. OSBORN 1930, The tree coryluses, Gard. Chron. 2250: 106-107); Cambridge Bot. Gard., 16 m. high, girth at base 3 m. (KASAPLIGIL 3427) — HUNGARY : Budapest, Ile Marguerite —trees 12-15 m. high (Herb. specimen collected in May 20, 1905, Conservatoire Bot., Geneva). — SWITZERLAND: Geneva, Univ. de Genève, Jardin des Bastions—tree 16 m. high with a single bole of 2,5 m. from ground, d.a.b.h. 42 cm., 100 years old, fruits sterile (KASA-PLIGIL 1963, Musées de Genève 4, 32 : 8-10); ibid., Jard. Bot., Rue de Lausanne—tree raised from a sucker, few stems from ground, 9 m. high, 20 years old, fruits sterile (ibid.); ibid, Arboretum, Ecole d'Horti-culture, Châtelaine—tree raised from seedling, height 6 m., single bole, d.a.b.h. 11 cm., 15 years old, fruits sterile (ibid.); St. Gallen, near the junction of Notker and Pelikan Str.— three young trees, each with a single bole, 9 m. high, d.a.b.h. 18 cm., 23 years old, sterile fruits, pos-sibly a clone (KASAPLIGIL no. 3415, Oct. 10, 1962); ibid., Zwinglistr., next to Kino Rex—a solitary tree with a single bole, 17 m. high, 40 years old, sterile fruits, some branches completely dead (KASAPLIGIL no. 3416, Oct. 10, 1962); Zürich, Bot. Gart. Univ. Zürich, facing Löwenstr.—single tree with a broad conical crown, 10 m. high, d. a. b. h. 32 cm., abundant staminate catkins often abnormally forked at tips, no fruits at all (KASA-PLIGIL no. 3376, July 25, 1962).

HISTOLOGY OF THE STEM

The transverse sections of stems one to three years old have been studied comparatively to bring out the anatomical similarities and dif-ferences among three species of *Corylus*. Young developing shoots at the stage of primary structure as well as one year old stems completing the secondary growth of the first year, are covered by soft unicellular simple trichomes, and long, stiff emergences. Various forms of these trichomes will be described in detail under the heading of "foliage leaves".

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On the shoot of *Corylus avellana* and *C. maxima*, the trichomes partly persist through the second year's growth, while the trichomes on the young shoots of *C. colurna* are completely shed towards the completion of the first year's secondary growth. All three species possess an uniseriate epidermis. In *C. avellana* and *C. maxima*, the outer tangential walls of the epidermal cells are moderately cutinized, while in *C. colurna* a heavy cutinization is apparent. The epidermis is partly sloughed away from three years old stems of *C. avellana* and *C. maxima*, but some trichomes remain attached to its remnants. At the comparable stage, the epidermal tissue of *C. colurna* is completely sloughed away from the stems.

Phellogen develops from the outermost layer of the cortex. Phellem consists of 5-7 layers of small and moderately compact cells in one year old stems of *C. avellana* and *C. maxima*. The phellem tissue in a one year old stem of *C. colurna* consists of 7-10 layers of cells, the inner layers being much compressed, the outer ones showing very large but more or less regular cells. The lenticles are well developed at the end of the first year.

The cortex differentiates into outer collenchymatous and inner parenchymatous regions. Collenchyma consists of 5-7 layers of compact cells without inter-cellular spaces. The collenchyma cells contain chloroplasts, starch grains and tanniferous material. Occasionally, the cells of the innermost layer of collenchyma contain prismatic crystals of calcium oxalate. The collenchymatous ring in *C. avellana* and *C. maxima* becomes interrupted as a result of secondary growth, the gaps between the collenchyma groups being occupied by thin-walled parenchyma cells. In three years old stems of *C. colurna*, however, collenchyma remains as a continuous cylinder.

In one year old shoots of *C. avellana* and *C. maxima* 4-5 cell layers of cortical parenchyma underlie the collenchyma tissue, while in *C. colurna* 5-10 cell layers are observed. The cortical parenchyma cells are primarily chlorophyllous, but cells containing either tanniferous material or druses of calcium oxalate, are not uncommon.

The phloic sclerenchyma adjacent to the inner boundary of the cortex, consists of a continuous cylinder 2-7 layers of fibers in the shoots that are one year old. This cylinder of fibers becomes broken as the growth in thickness advances. The brachysclereids develop from the cortex as well as from the phloem parenchyma cells in the interrupted regions and complete the cylinder of sclerenchyma. The lumina of the fibers are highly reduced, but those of the brachysclereids are quite large and often contain solitary prismatic crystals of calcium oxalate. In *C. avellana* and *C. maxima*, the phloic sclerenchyma is more or less equally thick throughout the cylinder, but in *C. colurna* the patches of brachysclereids are nearly twice as thick as the rest of the fiber cylinder.

The sieve tube elements of the protophloem become obliterated, while the metaphloem cells are somewhat compressed, but not crushed. Some of the phloem parenchyma cells contain druses of calcium oxa-

late. Tannic substances occur in many of them. The secondary phloem is quite similar to that in *Tilia* stems (cf. ESAU 1953, p. 395); it becomes banded by the formation of secondary phloem fibers. The cells containing mucilaginous and tannic substances are abundant in dilating phloem rays. The brachysclereids occur commonly in clusters or individually within the secondary phloem of *C. colurna* while they are rare in *C. avellana* and *C. maxima*.

In all three species, the wood is diffuse porous. The growth layers are sharply demarcated at their boundaries. Several growth layers were observed within a single annual ring in the stem wood of *C. maxima*. Due to the presence of aggregate rays, the growth layers are distinctly wavy in *C. avellana* and *C. maxima* while in *C. colurna* they are straight or obscurely wavy. The bulk of the secondary xylem consists of relatively thin-walled imperforate tracheary elements in *C. avellana* and *C. maxima* and of vessel elements and thick-walled tracheids in *C. colurna*. The vessel members form radiating rows, 2-10 cells in *C. avellana* and 2-12 cells in *C. maxima* and 2-6 cells in *C. colurna*. The aggregates of 2-5 pores occur in the spring wood of *C. avellana* and *C. maxima*. In *C. colurna*, pore aggregates consisting of 2-12 cells form 2-3 rows expanding tangentially. The cross-sectional outline of the vessel members is mostly polygonal, rarely rectangular in *C. avellana* and *C. maxima* while it is often rectangular and less frequently polygonal in *C. colurna*. The xylem rays are mostly uniseriate, seldom biseriate in *C. avellana*, all uniseriate in *C. maxima* and 1-3 seriate in *C. colurna*. As an average, there are 21 xylem rays per milimeter of stem section of *C. avellana* and *C. maxima* and 16 xylem rays per milimeter of stem cross-section in *C. colurna*. The heights of the xylem rays vary from 5 to 30 cells, but rays up to a height of 80 cells occur as the result of ray fusion in *C. avellana* and *C. maxima*. The xylem rays of *C. colurna* are 7-15 cells in height, or up to 50 cells or even more by fusion. With respect to the distribution of wood parenchyma, the stem sections of *C. avellana* and *C. maxima* again present a striking similarity. Both of these species have an apotracheal diffuse type of parenchyma which often becomes a metatracheal type (banded) in or near the summer wood of the growth layers. The wood parenchyma of *C. colurna* is apotracheal diffuse, often clearly metatracheal, seldom paratracheal scanty.

In all three species, the pith consists of an outer medullary sheath (EAMES and MAC DANIELS 1947) of thick-walled, elliptical small cells and an inner region of thin-walled, polyhedral, large cells. The cell size in the medullary sheath ranges from 8 to 41 microns. These cells bear prominently conspicuous simple pits on their walls and contain a large number of simple and compound starch grains. The medullary sheath was stained very deeply with safranin in all stem preparations. Central pith parenchyma cells vary from 35 to 105 microns and contain solitary or clustered crystals of calcium oxalate. The druses occur either singly or in pairs in the idioblasts, completely filling the cell cavity which seems to be devoid of protoplasm and starch grains; or they occur in large

pith parenchyma cells occupying 1/3 to 1/5 of the lumen and being accompanied by starch grains.

Calcium oxalate druses show considerable size variation from one species to the other and in different tissues of the same species. Fourty druses have been measured from the cortex, secondary phloem and pith of each species in order to study the size variation. The result of these measurements is summarized in Table I. The first figures represent the average values and the parenthetical figures show the minimum and maximum values for the longest axis of druses.

TABLE I. — COMPARISON OF THE SIZES (IN MICRONS)
OF CALCIUM OXALATE DRUSES FROM 3-YEARS OLD STEMS

TISSUES	Corylus avellana	Corylus maxima	Corylus colurna
CORTEX	24.1 (16.9-33.8)	22.9 (10.4-41.6)	38.8 (20.8-67.6)
SECOND PHLOEM	11.7 (7.8-18.2)	12.7 (7.8-23.4)	15.0 (9.1-26.0)
PITH	22.9 (13.0-31.2)	21.7 (13.0-36.4)	26.5 (15.6-33.8)

A glimpse at the table shows the fact that in all three species the cortical druses are the largest ones, but those of the secondary phloem being the smallest ones. The average sizes of druses calculated from three different tissues of C. avellana and C. maxima are fairly close to each other, while the average sizes of druses in C. colurna are much larger than those of the former species. Likewise, the size fluctuation, particularly with respect to cortical druses, is very prominent in C. colurna. The frequency of the size classes are presented in three histograms (Fig. 1, A-C). The size classes of druses are indicated along the horizontal lines in terms of decimal groups, the frequencies of size classes along the vertical lines in terms of percentages. The size classes of phloem and pith druses fall into three groups (Fig. 1, A-B), those of the cortical druses into six groups (Fig. 1, C). The frequencies of the size classes follow each other fairly closely in C. avellana and C. maxima. The size classes of druses and their frequencies particularly in the cortical tissue of C. colurna (Fig. 1, C) fluctuate widely showing a pronounced deviation from those of C. avellana and C. maxima. The size of the calcium oxalate druses seems to have a diagnostic value at least for distinguishing C. colurna from the other two species. A broad survey of the occurrence and size variations of druses in other organs and tissues as well as a comparative survey of other species of Corylus may lead to finding further diagnostic features along this line.

SECONDARY XYLEM ELEMENTS: Certain characteristics of the xylem elements as observed in transverse sections of the stems were already

described above. The reader is also referred to the recently published atlas of GREGUSS (1959) for the descriptions and illustrations of the radial, longitudinal and tangential sections of the stem wood as well as of the wood elements. However, it was inevitable to survey the material in
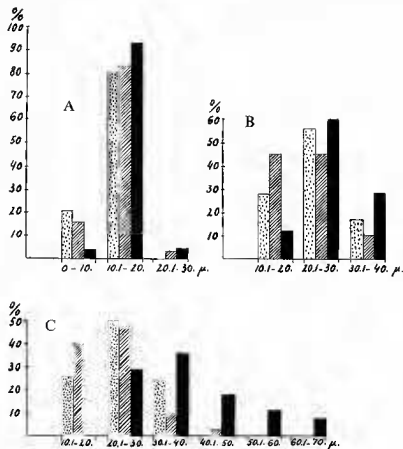

Fig. 1. — Histograms showing the frequencies of the size classes of calcium oxalate druses in stem tissues of three species of *Corylus*. Size classes in microns are indicated along the horizontal lines, their frequencies on the vertical lines. The stippled columns represent *Corylus avellana*, shaded columns *C. maxima* and the solid black columns stand for *C. colurna*. **A**, Druses of the secondary phloem; **B**, Druses of the pith parenchyma; **C**, Druses of the cortical parenchyma.

macerated state in order to study the size variation and the structural features of the secondary xylem elements.

The vessel members of all three species bear scalariform perforation plates. Vessel members with a simple perforation plate, occur often in *C. colurna*, very rarely in *C. maxima*. The end walls of the vessel

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members are usually tapering, but rounded tips occur also. In some of the vessel members, one end may be pointed while the other may be rounded. The perforation plates are always sloping. The degree of obliqueness is more pronounced in the vessel members of *C. maxima* than in those of the other two species. Long, tapering, ligulate tips are characteristic for the vessel members of all three species. Bordered pits are crowded, particularly on the tangential walls, being often arranged in alternate, less frequently in reticulate patterns. The bordered pits of the vessel members in *C. colurna* are often expanded horizontally and arranged in a scalariform pattern resembling scalariform perforation plates. Reduced, slit-like bordered pits seem to be restricted to the vessel members of *C. maxima* only. The apertures of these pits are oblique with respect to the longitudinal axis of the vessel members. Helical tertiary thickenings in vessel members are found in all three species, although rather rarely in *C. maxima*. Vessel members intermediate between tracheids and true vessel elements occur in *C. avellana* and *C. colurna*. Such elements are very similar to tracheids with respect to their form and pitting, but they usually bear a single perforation plate on their lateral walls.

I have not seen any vessel member with reticulate perforation plates, but certain vessel members of *C. colurna* and *C. maxima* bear scalariform perforation plates with forking (simple branching) bars. The number of bars in the perforation plates varies even between two perforation plates of the same vessel member. However, the average number of bars and their minimum and maximum extremes seem to have diagnostic importance in the species concerned. I counted the bars of fifty perforation plates from each species. The number of bars varies from 3 to 10 in *C. avellana*, the average number being 6. The perforation plates in *C. maxima* have between 1-9 bars, averaging 5. These figures are fairly close to each other in the two species just named. In *C. colurna*, however, the average number of bars is 9, fluctuating from zero to 27. The frequencies of perforation bars in three species of *Corylus* are presented in a histogram (Fig. 2). The number of bars are marked along the horizontal line, their frequencies along the vertical line. This histogram shows that the vessel members bearing plates with seven bars occur most frequently in *C. avellana*; perforation plates with six and eight bars being next in frequency. In *C. maxima*, the most frequent number is five, the perforation plates with six and four bars coming next. The frequencies of bar numbers in *C. colurna* show two separate peaks, i. e. perforation plates with six bars occur most frequently, those with twelve bars being next. *C. avellana* and *C. maxima* show certain similar aspects while the frequency curve for *C. colurna* differs strikingly from both other species.

Tracheids are characterized by their tapering outlines, pointed tips and crowded, alternating bordered pits. The walls of the tracheids are evenly thick. In *C. maxima*, the tracheids sometimes exhibit rounded tips associated with a short ligula. Furthermore, the bordered pits of

the tracheids in this species are somewhat expanded laterally, resulting in face view in a slightly elliptical outline. A clear-cut distinction of the tracheids in *C. colurna* is not always possible due to the presence of imperforate elements, intermediate between tracheids, fiber tracheids and libriform wood fibers.

Fiber tracheids are evenly thin-walled, prosenchymatous cells bearing bordered pits with slit like apertures in all three species; they
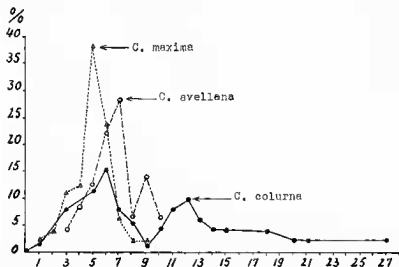

Fig. 2. — Histogram showing the frequencies of the perforation bars in the vessel members of three species of *Corylus*. The bar numbers are indicated along the horizontal line. Empty circles connected with dashed lines stand for *Corylus avellana*, triangles connected with dotted lines represent *C. maxima*, and solid circles connected by continuous lines represent *C. colurna*.

are the most abundant elements of the secondary xylem in *C. avellana* and *C. maxima*. Fiber tracheids with ligulate tips occasionally occur in *C. maxima*. The tips of the fiber tracheids in *C. colurna* are sometimes shaped irregularly. Most likely, such irregular tips deviating from regular slender tips result from the intrusive growth of the tips. The lateral walls adjacent to parenchyma cells are conspicuously cornered in *C. colurna*.

Libriform wood fibers are thick-walled; their pointed tips are occluded during secondary sclerosis. They bear highly reduced, oblique vestigial pits in *C. avellana* and *C. maxima* and possess simple pits or straight walls without pits in *C. colurna*. In the latter case, some wood fibers occasionally appear with minute transverse lines which may represent horizontally broadened, but eventually reduced simple pits.

Wood parenchyma consists of rectangular or tapering vertical elements with lignified, thick walls and simple pits. In *C. maxima*, they

WOOD ELEMENTS	*Corylus avellana*	*Corylus maxima*	*Corylus colurna*
Vessel members	404 (194-518) × 27 (13-39)	352 (275-486) × 31 (16-47)	251 (128-453) × 24 (16-31)
Tracheids................................	428 (324-486) × 22 (16-29)	378 (308-502) × 16 (10-21)	244 (113-437) × 16 (10-23)
Fiber tracheids	567 (372-842) × 17 (12-30)	486 (389-680) × 16 (10-26)	360 (194-567) × 12 (8-16)
Libriform wood fibers	657 (518-778) × 8 (5-10)	631 (486-729) × 8 (5-10)	623 (518-730) × 8 (5-10)
Wood parenchyma..........................	97 (78-114) × 10 (7-13)	64 (36-124) × 7 (4-13)	53 (36-78) × 11 (8-13)
Ray parenchyma	28 (16-38) × 25 (16-32)	36 (24-44) × 24 (13-36)	27 (21-36) × 18 (8-29)
Brachysclereids in xylem rays	none	none	18.5 (12.0-26.2)

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are very narrow and resemble septate fibers, but a careful examination shows that they actually form superimposed vertical series. Fusiform parenchyma cells (Committee on Nomenclature, International Association of Wood Anatomists 1957, p. 16) are found in C. avellana. Some "supplementary fibers" (= Ersatzfasern in Greguss 1959, p. 17) occur in C. colurna. These living cells resemble fiber tracheids in outline, but are very short and bear simple pits and slit-like, oblique bordered pits on their thick secondary walls.

Ray parenchyma consists of rectangular cells with thick walls in C. avellana and C. maxima, and relatively thin walls in C. colurna. The marginal cells of the rays are wedge-shaped. Some of the ray parenchyma cells of C. colurna contain solitary crystals of calcium oxalate. The secondary xylem of C. colurna differs considerably from the other two species due to the presence of brachysclereids, particularly in multiseriate rays. These brachysclereids are characterized by conspicuously lamellated walls with ramifying pit canals and highly reduced lumina. Some of them are cubical, but many of them exhibit also irregular shapes. Their diameters vary from 12.0 to 26.2 microns, averaging 18.5 microns.

The sizes of wood elements are summarized in Table II. For obtaining the length dimensions, the tracharey elements were measured from tip to tip. The average measurements are based on 15-20 measurements for each element. The first figures given for each wood element represent the average length, followed by minimum and maximum lengths in parentheses. The second set of figures separated by (X), represents the average widths of wood elements (with the exception of ray parenchyma cells), followed by minimum and maximum widths in parentheses. The second set of figures given for the ray parenchyma represents the heights of these cells.

C. avellana has the longest wood elements, C. maxima possesses shorter ones; the shortest elements are found in C. colurna as seen in Table II. In other words, there is a progressive decrease in the length of wood elements from C. avellana through C. maxima to C. colurna. One expects to find a progressive increase in the width of the wood elements parallel to the sequence of reduction but this is not the case. On the contrary, the average width of vessel members tracheids and fiber tracheids in C. colurna is smaller than widths given for these elements in C. avellana. In all three species, the width of libriform wood fibers is constant. The length of wood parenchyma cells shows a definite reduction from 97 microns in C. avellana to 64 microns in C. maxima and to 53 microns in C. colurna, but their widths (10, 7 and 11 microns respectively) do not show any sequence towards reduction or increase. Although the dimensions of wood elements exhibit much variation in each species, the figures given for the widths of wood elements in C. colurna and C. maxima are fairly close to one another.

MORPHOLOGY AND HISTOLOGY OF THE FOLIAGE LEAVES

The leaves are simple, alternate, dark-green above, pale green beneath. Very young leaves, while enclosed within the buds are folded along the midribs and accompanied by stipules (EICHLER 1878, 2: 16, fig. 7 E). At this stage, the leaves are almost entirely covered with soft silvery grey hairs. As the leaves emerge from the buds, they unfold and expand, loosing their stipules as well as most of the hairs even before reaching the ultimate mature size. However, the hairs remain along petioles and major veins on the abaxial side of the leaves. The leaves of *C. avellana* and *C. maxima* are quite similar to one another, in both species being roundish ovate to broad ovate in outline, abruptly acuminate at apex and cordate at base. The margins are doubly serrate and slightly lobulate. The lamina is 5-12 cm. long, 3-10 cm. broad in *C. avellana*: 7-14 cm. long and 5-10 cm. broad in *C. maxima*. The leaves of *C. colurna* are ovate to broadly ovate, very rarely obovate in outline, acute to cuspidate at apex and cordate to oblique cordate at base. Margins are doubly serrate or crenate serrate, often lobulate. The lamina is 5-19 cm. long and 5-14 cm. broad.

TRICHOMES: Particularly young developing organs are densely covered by various types of trichomes derived either directly from the epidermis or both from epidermis and cortex. Most trichomes are shed as the organs mature, but a considerable amount of trichomes remains on the veins of the abaxial leaf surfaces, around petioles and young twigs, on the involucral bracts and at the nut tips. Trichomes on the foliage leaves of *Corylus* species under study present the following types:

1) *Unicellular simple trichomes*, varying in length from 40 to 143 microns. These trichomes have a bulbous base usually embedded in the epidermal layer and a long, gradually tapering body terminating in a pointed tip (Fig. 3, F). The lumen is completely reduced in the upper 1/2-2/3 portion of the body as the result of secondary wall thickening. The basal portions of simple trichomes often retain the protoplast.

2) *Septate simple trichomes*, being very similar to the first type, but at the basal portions showing a multicellular condition, resulted from cell divisions within the reduced lumen after the secondary wall formation in the originally unicellular trichome has taken place. Septate simple trichomes also have a bulbous base embedded in the epidermal layer and a tapering body having 2-4 cells at its 1/3-1/4 basal portion. The upper portion of the body consists of a secondary wall without lumen (Fig. 3, E). The septations of these trichomes are much thinner than the lateral walls and do not exhibit secondary thickening. Septate simple trichomes are from 160 to 610 microns long, their average length being 390 microns in *C. avellana*, 413 microns in *C. maxima* and 295 microns in *C. colurna*. The cells of septate trichomes are living and contain some

chloroplasts. Obviously, septate trichomes of *Corylus* are very distinct from familiar multi-cellular unbranched trichomes such as the staminal hairs of *Tradescantia* in which the trichome consists of a single row of cells with equally thick primary walls.

3) *Tufted trichomes* which seem to be a cluster of unicellular simple trichomes. They are very similar to the tufted hairs of *Quercus* (cf. Esau 1953, p. 154, fig. 7, 8, C). This type is particularly abundant on the leaves and involucral bracts of *C. arellana* var. *grandis* and *C. maxima* var. *atropurpurea*.

4) *Capitate glandular trichomes* are multicellular but much smaller than unicellular—or septate simple trichomes. These trichomes consist of a short stalk and a head of radiating secretory cells (Fig. 3, A-D) which secrete a resinous substance. Their total length varies from 36 to 76 microns, average length being 57 microns in *C. avellana*, 49 microns in *C. maxima* and 52 microns in *C. colurna*. The diameter of the head measures, as an average, 30 microns.

5) *Club-shaped glandular trichomes*, also multicellular, usually occurring along veins of the abaxial leaf surface (Fig. 3, H). These trichomes are 42 to 70 microns long and 14 to 39 microns thick in the upper portion of the body which tapers towards the base. On top, they bear 1-4 secretory cells.

6) *Conical glandular trichomes*, 30-40 microns long and about 25 microns thick at base, tapering slightly towards the apex (Fig. 3, 1). These trichomes seem to represent a type intermediate between trichomes and emergences since the base of the conical trichomes is formed by divisions of subepidermal cells (cf. Netolitzky 1932). Conical glandular trichomes occur in *C. colurna* more commonly than in the other two species.

7) *Glandular emergences* with a long, conspicuous body derived from epidermal and subepidermal layers and a head consisting of many secretory cells. Resinous and mucilaginous secretions accumulate on the head and appear dark brown to black. These glandular emergences are from 0.4 to 3 mm. long, but in *C. colurna* var. *glandulifera* they measure up to 4 mm. The head diameter varies from 50 to 195 microns. A noteworthy feature of these glandular trichomes is the fact that they are photo-synthetic. The ground tissue as well as the epidermis of the emergences contain chloroplasts (Fig. 3, G). Spicular trichomes which represent the most abundant trichome type in *C. rostrata* Ait. var. *californica* A. DC. are not present in the species I am dealing with in this paper.

Epidermis: The epidermis is uniseriate, bearing a cuticle 2 microns thick. There are certain pronounced differences between the juvenile
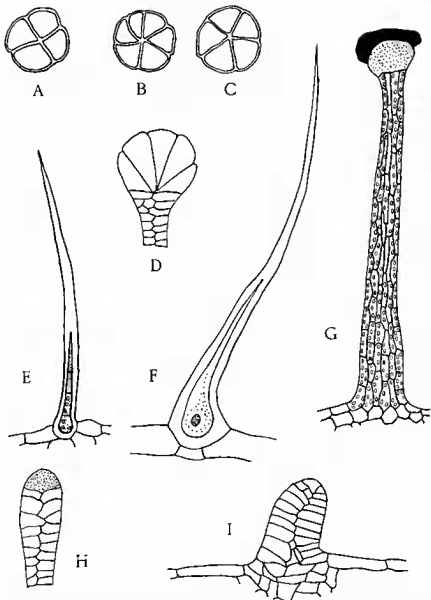
Fig. 3. — Camera lucida drawings showing the types of trichomes which occur in *Corylus* leaves ; **A-C,** Top views of capitate-glandular trichomes from the petiole of *Corylus avellana* showing the radiating secretory cells, 1 000 × ; **E,** A unicellular simple trichome from the abaxial side of a leaf of *C. avellana,* 335 × ; **F,** A septate simple trichome from the petiole of *C. colurna,* 335 × ; **G,** A glandular emergence of *C. colurna.* Glandular head is stippled, secretory deposit in black. 230 × ; **H,** A club-shaped glandular trichome from the leaf of *C. avellana,* 1 000 × ; **I,** A conical glandular trichome from the leaf of *C. colurna,* 1 000 × .

leaves of seedlings and the mature leaves of adult plants with respect to the form of the epidermal cells proper. Seen in face view, the anticlinal walls of the epidermal cells are undulate on the abaxial as well as adaxial sides of the fully grown juvenile leaves (fig. 4, A-C, fig. 5, F). The abaxial epidermal cells are usually elongated in one direction; their length varies from 28 to 75 microns as measured in face view. The stomata are confined to the abaxial surface and distributed irregularly. They are of ranunculaceous type and each stoma is accompanied by 4-6 subsidiary cells (Fig. 4, A and C). This type of stomata is designated as anomocytic type by METCALFE and CHALK (1957, vol. I, P. XV.). The anticlinal walls of the subsidiary cells are mostly straight in juvenile leaves and usually smaller than the adjacent epidermal cells (fig. 4, C). The stomata are situated at the same level as the epidermal cells. The length of the guard cells ranges from 23 to 29 microns, the width from 7 to 10 microns. The adaxial epidermis of juvenile leaves also exhibit undulations although this feature is less pronounced in C. avellana (fig. 4, B) than in C. maxima and C. colurna. Adaxial epidermal cells in the juvenile leaves of C. avellana and C. maxima measure 39 to 65 microns in length and 13-28 microns in width as seen in face view. The ratio between the epidermal cells and the underlying palisade parenchyma is either 1/8 or 1/9 in both species (fig. 4, B). The adaxial epidermis of the juvenile leaves of C. colurna is quite heteromorphic due to the presence of more or less isodiametric undulate, stellate and rectangular cells, the last type being restricted to the regions along major veins. The diameters of the cells vary from 26 to 36 microns as measured in face view. Palisade parenchyma cells are divided lengthwise, the daughter cells remaining attached in pairs (fig. 5, F). The ratio between epidermal cells and palisade parenchyma cells is 1/22.

The abaxial epidermal cells of mature leaves from adult plants are characteristically undulate, but the adaxial epidermal cells are rectangular (in C. avellana and C. maxima) or polygonal (in C. colurna) with straight anticlinal walls. In C. colurna, the abaxial epidermis of adult leaves also has typically stellate cells with 4-6 arms extending radially (fig. 5, G). Stellate epidermal cells were not observed in C. avellana and C. maxima. The undulated epidermal cells are elongated in one direction, measuring from 18 to 57 microns in face view. The subsidiary cells of stomata may be straight walled or undulate. They contain mucilaginous substances (fig. 4, D and fig. 5, G). The dimension range of guard cells is the same as stated earlier. The stomata are slightly raised above the surface of the epidermal layer in C. avellana, but appear at the same level with the rest of the epidermis in C. maxima and C. colurna as seen in transverse leaf sections. The outer ledges of the guard cells are well developed forming a front cavity, but the inner ledges are hardly detectable in transections.

Adaxial epidermal cells of the adult leaves vary considerably in form (fig. 5, E and H), but the anticlinal walls are mostly straight. Mucilaginous epidermal cells are distributed at random, however, elongated
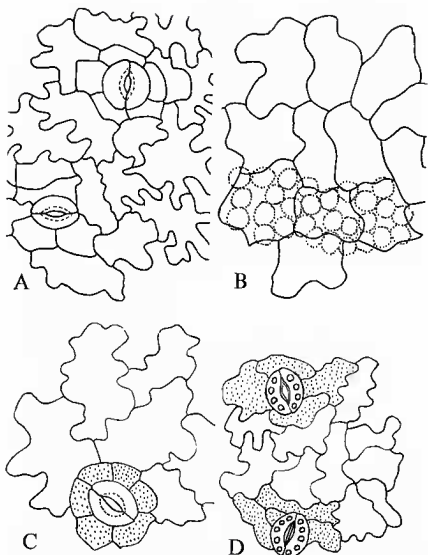
Fig. 4. — **A-D**, Camera lucida drawings of epidermis as seen in face view; mucilaginous subsidiary cells are stippled. All drawings 800 ×. — **A**, Abaxial epidermis of the juvenile leaf from a seedling of *C. avellana*; **B**, Adaxial epidermis of the juvenile leaf of *C. avellana*; dotted circles represent top views of palisade cells; **C**, Abaxial epidermis of the juvenile leaf from a seedling of *C. maxima*. Note straight walls of subsidiary cells; **D**, Abaxial epidermis from the mature leaf of an adult plant of *C. maxima*. Note undulated walls of subsidiary cells.

rectangular cells over major veins always contain mucilaginous substances (fig. 5, E). Epidermal cells which are in contact with idioblasts containing calcium oxalate druses exhibit prominent wall thickenings all around. The length of the adaxial epidermal cells extends from 18 to 57 microns and their width from 9 to 28 microns. The ratio between epidermis and palisade varies from 1/8 to 1/14 in *C. avellana* and from 1/7 to 1/17 in *C. maxima*. This ratio varies from 1/11 to 1/13 in *C. colurna* which is fairly close to the half of 1/22 ratio given for the juvenile leaves of this species. Undivided palisade cells of adult leaves explain this correlation (cf. fig. 5, F and H).

MESOPHYLL: Commonly a single layer of cells constitutes the palisade on the adaxial side, but the sun leaves show the tendency to form a regular second layer. The palisade occupies 1/4 of the leaf thickness. Idioblasts containing calcium oxalate druses occur in the palisade layer. Such cells appear as bright dots when a leaf is examined with a hand lens against a light source. FOSTER (1956) in his classification of plant idioblasts, has included these idioblasts under "excretory idioblasts". The spongy parenchyma consists of cells irregularly shaped, with prominent intercellular spaces between. It occupies 1/2 of the leaf thickness. Druses and solitary crystals occur in spongy parenchyma.

VASCULAR SYSTEM : The primary vein which traverses the lamina from base to tip projects prominently on the abaxial side of leaf. This midrib is hairy on both sides of the leaf, but more densely so on the lower side. The vascular bundle of the midrib is collateral; it appears crescent-shaped or closed cylindrical in transections. A limited amount of secondary growth takes place in the vascular strand of midribs. In transectional view, the tracheary elements are arranged in radial rows. The sclerenchymatous sheath around the bundle is a continuous tissue. In crescent-shaped vascular bundles, the bundle sheath sclerenchyma reaches the edges of the crescent and partly invades the parenchymatous pith of the bundle in *C. avellana* and *C. maxima*. In *C. colurna*, however, fibers of the sclerenchyma sheath reach the "mouth" of the crescent, but de not "enter" the pith. Subepidermal collenchyma is well developed on both abaxial and adaxial sides of the midrib. Large parenchyma cells containing chloroplasts and calcium oxalate crystals, constitute the cortex between collenchyma and sclerenchyma tissues. The secondary and tertiary veins are enclosed by the bundle sheath. These veins also project on the abaxial side of the leaf. Bundle sheath extensions which are strongly developed in *C. avellana* and *C. maxima* consist of 1-3-cell layers of lignified sclerenchyma and connect the veins with upper and lower epidermises. In *C. colurna*, however, bundle sheath extensions are only weakly developed and the thick-walled sclerenchyma cells are not lignified.

The pattern of major venation in *Corylus* leaves is craspedodromous (ETTINGHAUSEN 1861), i.e. secondary veins follow a direct course towards
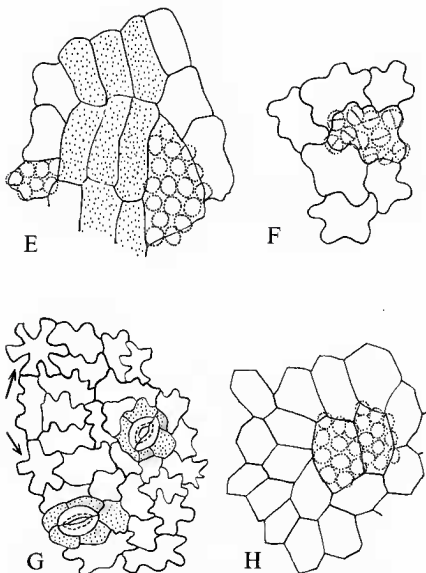
Fig. 5. — **E-H**, Camera lucida drawings of epidermis as seen in face view; mucilaginous epidermal and subsidiary cells are stippled. All drawings 800 ×. — **E**, Adaxial epidermis of a mature leaf from an adult plant of *C. maxima*; dotted circles represent top views of underlying palisade cells; **F**, Adaxial epidermis of the juvenile leaf from a sucker of *C. colurna*; the top view of the underlying palisade cells is shown with dotted circles divided in halves, i. e. each circle represents a pair of palisade cells remaining attached; **G**, Abaxial epidermis from the mature leaf of an adult plant of *C. colurna*; stellate epidermal cells are indicated by arrows; **H**, Adaxial epidermis from mature leaf of *C. colurna* showing the polygonal epidermal cells and their relation to palisade cells beneath; each dotted circle represents a single cell as contrasted with a pair of cells in Fig. 5, F.

the leaf margin and terminate in marginal lobes. The veins of the first, second and third categories are considered to constitute the major venation of leaves (PRAY 1954). The pattern of major venation is essentially similar in juvenile and adult leaves. The secondaries are rarely opposite near the lamina base, but mostly alternate each other along the primary vein resulting a typical pinnate venation pattern. The number of secondaries varies between 7 to 9 pairs in *C. avellana* and *C. maxima* and between 5 to 12 pairs in *C. colurna*. These variations in the number of secondaries hold true also for the smallest as well as the largest leaves examined in a wide range of herbarium material. Most likely, the variation in the dimensions of leaf blades resulted from an increase or decrease in the sizes of intercostal areas and ultimate areoles rather than an increase or decrease in the number of veins (PRAY 1955, a and b). In *C. avellana*, the secondaries near the lamina base diverge from the primary vein at an angle of 35—60º, those near the apex of lamina at an angle of 15—30º. The basal secondaries diverge at an angle of 45—95º, those near the blade apex extend at an angle of 15—30º in *C. maxima*. The basal secondaries in *C. colurna* are disposed of at 35—90º and the uppermost secondaries at 18—25º.

Tertiary veins diverge from the basiscopic side of secondaries at an angle of 25—35º and follow a slightly curved course towards the lamina edges, terminating in marginal teeth. Usually, there are 5 to 8 tertiaries extending unilaterally from the first pair of basal secondaries. The number of tertiaries fluctuates considerably between the members of the same pair of secondaries. The subsequent secondaries in acroscopic direction give rise to a progressively diminishing number of tertiaries. No tertiaries develop from the uppermost four to five pairs of secondaries. Tertiary veins bifurcate submarginally, branches running along the margin in short distances and giving rise to minor veins of the 4th, 5th and 6th categories. In juvenile leaves from seedlings and sucker shoots, the xylem of secondary and tertiary veins primarily contains spiral tracheary elements.

Minor venation of juvenile leaves exhibits certain anatomical differences from that of adult leaves. The description of minor venation in juvenile leaves given below is based on first juvenile leaves from young seedlings of *C. avellana* and *C. maxima* and the juvenile leaves produced by rare suckers of *C. colurna*. Strong similarity regarding morphology and venation patterns in seedling and coppice-shoot leaves of *Lacunaria* was described by FOSTER (1951). Hence, for the time being, I am using the sucker leaves of *C. colurna* for the comparison of minor venation of juvenile leaves while expecting to examine the seedling leaves of this species when such material becomes available to me.

Veins of fourth, fifth and sixth categories and vein endings (ultimate veinlets) which terminate freely in mesophyll, constitute minor venation that forms the reticulum. Quaternary and quinquenary veins often arise directly from secondary or tertiary veins, although generally, each category of vein gives rise to the veins of the subsequent category.
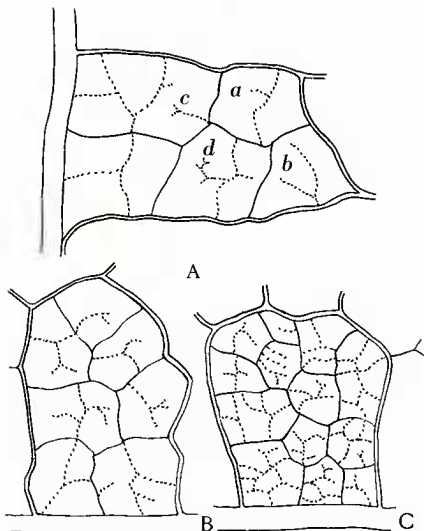
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Fig. 6. — **A-C**, Camera lucida drawings showing interquaternary panels and their subdivisions formed by minor veins in juvenile leaves. Broad double lines represent secondary veins, narrow double lines the quaternaries. Solid single lines indicate quinquenary veins. Veins of sixth category and vein endings are shown by dotted lines, 35 X. — **A**, from the first juvenile leaf of a seedling of *C. avellana*; *a* = an unbranched vein ending, *b* = a simple, basal dichotomy, *d* = a multiple dichotomy; **B**, from the first juvenile leaf of a seedling of *C. maxima*. Note the striking similarity with preceding figure; **C**, from a juvenile leaf of a sucker shoot of *C. colurna*. Note the prominent decrease of actual smallest distance from vein to vein, also the frequent formation of loops by the veins of sixth category.

Quaternary veins form interquaternary panels which are shown in fig. 6, A-C. Interquaternary panels are mostly polygonal, less frequently irregular rectangular. They are subdivided into a network of areoles formed by quinquenaries and veins of sixth category. Quaternaries which extend near the blade margins terminate in teeth. Interquaternary panels and their subdivisions are strikingly similar in *C. avellana* and *C. maxima* (fig. 6, A-B), except that the ultimate areoles are slightly larger in *C. avellana*. The long axis of interquaternary areoles varies from 324 to 1344 microns in *C. avellana*, from 372 to 994 microns in *C. maxima*, while the short axis measures from 194-405 microns in the former species and 226-421 microns in the latter. Ultimate areoles in *C. colurna* are considerably smaller, the long axis being 194-421 microns, the short one 145-324 microns. Furthermore, the ultimate areoles are somewhat loop-shaped, although many are polygonal. Vein spacing in juvenile leaves of *C. colurna* is much smaller than it is in the other two species.

Actually, vein endings represent branches of veins of sixth category, but they also arise from veins of lower categories. Vein endings may be unbranched or 1-3 times dichotomously branched. Repeated bifurcation usually involves only one shank of the veinlet. Dichotomous branching may either take place near the attachment of the veinlet to the vein of the preceding category or more distally (fig. 6, A). Unbranched vein endings are rather common in *C. colurna* (fig. 6, C). Ultimate tips of vein endings consist of one or two spiral tracheids accompanied by thin-walled prosenchymatous cells whose nature could not be determined in cleared material. The length of vein endings measures 129-680 microns in *C. avellana*, 128-583 microns in *C. maxima* and 111-428 microns in *C. colurna*.

Minor venation of adult leaves consists of vascular bundles of fourth, fifth, sixth and seventh categories and vein endings in all three species. The presence of an additional category of minor veins is a distinct feature from the vasculation of juvenile leaves. Apparently, veins of sixth category, described for juvenile leaves, branch further and give rise to veins of seventh category. The anastomosis of the latter is primarily responsible for the formation of the ultimate areoles. Quaternaries derived from secondaries traverse the intercostal areas and connect subsequent secondaries with each other. Interquaternary panels are often irregularly rectangular, rarely triangular or variously shaped as the result of branching of quaternaries. Interquinquenary areoles are irregularly rectangular or polygonal. Photomicrographs presented in fig. 7, A-D in part show interquinquenary areoles. In general, minor veins of adult leaves seem to branch and anastomose more frequently than those of juvenile leaves. Consequently, the vascular reticulum of adult leaves exhibit a very complicated pattern as seen in fig. 7, H especially. Ultimate areoles are delimited by veins of seventh category partially in collaboration with minor veins of other categories. Ultimate areoles are variously polygonal in shape, but may also be rounded as in *C. colurna*. In *C. avellana* and *C. maxima*, the ultimate areoles may or may not be provided
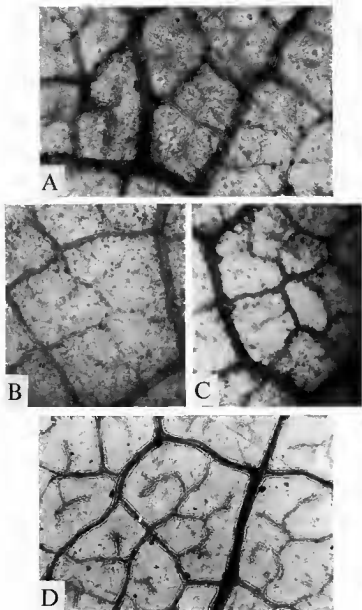
Fig. 7. — **A-D**, Photomicrographs showing anastomosis of minor veins and the structure of vein endings in cleared portions of adult leaves. Material was cleared in KOH solution and stained with safranin. Darkly stained heavy bundles are quinternary veins. 75 ×. — **A**, Minor venation of *C. avellana*. Interquinternary areoles are shown partly; **B**, Rectangular and triangular ultimate areoles in *C. maxima*. Note unbranched vein endings terminating blindly in the mesophyll of ultimate areoles; **C**, Polygonal areoles in *C. maxima*. Note hexagonal ultimate areole without a vein ending near the center of picture; **D**, A portion of an interquinternary areole and its subdivisions in *C. colurna*. Note dichotomous branching of vein endings and their curvatures.

with a vein ending, while in *C. colurna* most of them are provided with a freely terminating vein ending.

The length of ultimate areoles measures 162-350 microns in *C. avellana*, 194-437 microns in *C. maxima* and 178-518 microns in *C. colurna*. The width ranges from 48 to 168 microns in *C. avellana*, from 129 to 259 microns in *C. maxima* and from 81 to 243 microns in *C. colurna*.

Vein endings in mature leaves of *C. avellana* and *C. maxima* exhibit two types : the unbranched type, stout and straight, and the branching type, slender, bifurcating once or twice. The very tips of both types of vein endings consist of a cluster of short spiral tracheids surrounded by a sheath of large and isodiametric parenchyma cells. Terminal tracheids in *C. avellana* and *C. maxima*, are 25,0-39,6 microns long and 7,8-13,5 microns thick. Individual unbranched vein endings often anastomose and form triangular areoles between. The point of convergence between these bundles is crowded by numerous stout tracheids. Vein endings in adult leaves of *C. colurna* are rather long and slender. Unbranched veinlets occur there very rarely. If present, they are often horn-shaped. Branching veinlets bifurcate 1-3 times and the adjacent branchlets of two separate vein endings often anastomose and give rise to loop-shaped areoles (fig. 7, D). Veinlet tips in *C. colurna* consist of two spiral tracheids which are 20,8-52,4 microns long and 5,2-10,4 microns thick. Vein endings of *C. colurna* are ensheathed by isodiametric parenchyma cells. Occasionally, idioblasts containing druses of calcium oxalate are in contact with vein endings, but as far as I could observe, such idioblasts do not exhibit any particular pattern of distribution with respect to minor venation.

HISTOLOGY OF PETIOLES : Petioles are more or less cylindrical in form and densely pubescent or glandular-setose all around. Those of fully mature leaves of *C. colurna* loose most trichomes and emergences and become glabrous. The petiole length ranges from 5 to 18 mm in *C. avellana* and *C. maxima*. Petioles of *C. colurna* are much longer, ranging from 1 to 6 cm.

In this paper, the comparative histology of petioles is based on "Coupe caractéristique" (PETIT 1887), i.e. transverse sections through distal ends of petioles. However, transverse sections through the middle portions of petioles have also been examined in order to check, at different levels of the petioles, the structural variation of the vascular bundles. In *C. avellana* and *C. maxima*, the epidermal cells are relatively thin-walled. The outer tangential walls of epidermal cells are 2,6-3,9, radial walls 1,5-2 microns and the inner tangential walls adjacent to the subepidermal collenchyma 2,6-3 microns thick. The epidermal cell walls in the petioles of *C. colurna* are considerably thicker, lumina being reduced. The outer tangential walls of the epidermal cells in this species exhibit distinct laminations, their thickness varying from 5,2 to 10,4 microns. The radial walls are 2,6-3,9 microns, the inner tangential walls 3,9-5,2 microns thick.
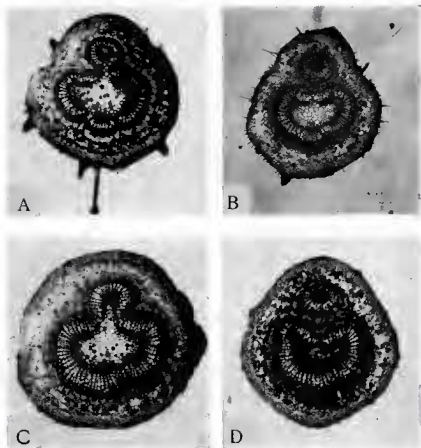
Fig. 8. — **A-D,** Photomicrographs showing transverse sections of petioles. All pictures are oriented with the adaxial side upward, 50 ×. — **A,** "Coupe characteristique" of *C. avellana*. Note tripartite condition on the abaxial side of the main bundle and the orch-shaped accessory bundle on the adaxial side. Dark projections around the section are the bases of broken glandular emergences, a complete emergence is extending on the lower side; **B,** "Coupe characteristique" of *C. maxima* showing the main vascular bundle with reniform outline and cylindrical accessory bundle; **C,** Transverse section through the middle-portion of the petiole of *C. colurna* showing the continuity of the main vascular bundle with the arch-shaped accessory bundle; **D,** "Coupe characteristique" of the same petiole of *C. colurna*, showing the cylindrical form of the accessory bundle and the reniform outline of the main vascular bundle.

Cortical collenchyma consists of 4-7 layers of cells with equally thickened walls. Collenchyma cells contain chloroplasts and starch grains throughout; the innermost cells contain crystals of calcium oxalate in addition. Collenchyma cells are capable of regeneration. Cork cambium originates from the middle layer of cortical collenchyma, giving rise to a periderm of several cell layers in places where the epidermis is torn as the result of secondary growth in the vascular bundle of the petiole.

Cortical parenchyma has 5-8 cell layers. Idioblasts containing druses of calcium oxalate and cells containing phlobaphene compounds are abundant. In *C. colurna*, the innermost cells of the cortical parenchyma bordering the sclerenchyma ring are thick-walled and transversely elongated. In *C. maxima*, however, innermost one or two layers of cells contain tannic material and form a dark sheath around the sclerenchyma ring.

The vascular tissue of the petiole forms a closed bundle, elliptical or reniform in outline. The main vascular bundle at the level of the " coupe caractéristique " is accompanied by an arch-shaped accessory bundle in *C. avellana* (fig. 8, A) and by a closed cylindrical bundle in *C. maxima* (fig. 8, B) and *C. colurna* (fig. 8, D) on the adaxial side. A tripartite condition on the abaxial side of the main vascular bundle is evident in *C. avellana* (fig. 8, A). This situation may result from the fusion of the originally separate three vascular traces (KASAPLIGIL 1951, p. 159). The transverse section through the middle portion of the petiole in *C. colurna* (fig. 8, C) shows a striking resemblance to the "coupe caractéristique" of *C. avellana*, including the tripartite appearance of the main vascular bundle. In all petioles examined, the tracheary elements are arranged radially. Xylem rays are 1-3 seriate. The phloem tissue is oriented exterior to the xylem tissue resulting a typical collateral arrangement. The main vascular bundles as well as the accessory ones are ensheathed by strongly developed sclerenchyma which consists of 4-7 fiber layers. The continuity of phloem tissue as well as of the sclerenchyma sheath is interrupted by dilating phloem rays which consist of highly lignified and thick-walled cells. The pith parenchyma of the bundles contains starch grains and variously formed crystals of calcium oxalate.

The "coupe caractéristique" taken from the petiole of juvenile leaves of *C. colurna* exhibits a complicated vascular system. Additional accessory bundles are situated on the lateral sides of the main vascular bundle. Lateral accessory bundles vary considerably in size and structure. They may be either closed cylindrical bundles similar to the adaxial accessory bundle or variously arch-shaped.

STAMINATE FLOWERS AND POLLEN

The genus *Corylus* is monoecious. Staminate flowers are arranged helically in drooping cylindrical catkins which develop either laterally from the axils of the fallen leaves or terminally on the previous year's

shoots. Staminate catkins form tassel-like clusters. At maturity, the individual catkin's length measures 3-6 cm in *C. avellana*, 5-7 cm in *C. maxima* and 5-12 cm in *C. colurna*. The number of staminate catkins varies from 2-4 in *C. avellana* and *C. maxima* and from 2-7 in *C. colurna*. The thickness of male catkins at the time of pollen shedding, ranges from 4 to 8 mm in *C. avellana* and *C. maxima*, and from 10 to 14 mm in *C. colurna*.

Staminate flowers are rather simple since they lack perianth. Each flower unit consists of 4-8 stamens in *C. avellana*, 4-10 stamens in *C. maxima* and 6-8 stamens in *C. colurna*. The stamens of *Corylus* are considered as "divided stamens" throughout the literature since individual anthers consist of two microsporangia. ENGLER and PRANTL (1894 p. 43, fig. 30) illustrate such a divided stamen with a filament splitted halfway, each branch bearing a bisporangiate anther. I had to dissect hundreds of staminate flowers in the course of preparing a series of slides in a study of meiosis in pollen mother cells of several species of *Corylus* and I was paying particular attention to each a divided filament. All staminate flowers I examined from various sources had undivided single filaments, each bearing a bisporangiate anther with a tuft of unicellular trichomes on top. EICHLER (1875) considered the lengthwise division of stamens in *C. avellana* as being complete, i.e. all the way down to the base of filaments. In such a case, one would expect to find each pair of "half filaments" either joined at base or at least opposite to each other. So far, I have not seen such an orderly disposition with respect to the filament. Excellent detailed illustrations of flowers can be found in REICHENBACH'S (1849-1850) Flora, in which the filaments are shown as unforked appendages. So far as I am aware, these "divided stamens" are not thoroughly investigated from the point of ontogenesis and I believe such a study may lead to reliable evidences toward understanding the morphological nature of stamens in *Corylus*. Provisionally, I consider each filament with its bisporangiate anther as a unit of "stamen". The number of stamens per flower fluctuates in different plants as well as in a single inflorescence. A specimen of *C. avellana* I collected in Paris had flowers with 5, 6, 7 and 8 stamens in the same inflorescence. A single catkin of *C. maxima*, also from the same locality, had terminal flowers with 4 stamens while the basal flowers of the same catkin had 8 stamens. Another *C. maxima* from Paris had 10 stamens per flower which was a constant number in different catkins of the same plant. Male flowers of a cultivated *C. colurna* in Zürich had 8 stamens as the most common number, but a herbarium material of the same species collected from China most commonly had 6 stamens per flower. Dehiscence of anthers is longitudinal. Stamens are adnate to bracts through the basal portions of their filaments.

Each flower is subtended by two small prophylls and a bract. Prophylls also, are adnate to the bract at their bases; their tips are free. Usually, both prophylls are equal in length, but occasionally one of the prophylls is shorter than the other.

Interesting teratological formations of staminate flowers were reported by HJELMQVIST (1948). According to this author, one or two stamens may be "transformed" into carpels, resulting bisexual flowers in *C. colurna*. He also describes the occurrence of a structure intermediate between a stamen and a carpel from the male flowers of the same species. I observed androgynous catkins in *C. maxima* in a plant growing in the Botanical Garden of Geneva. Some staminate catkins of this plant had several pairs of pistillate flowers at the tip of the catkins. A cultivated *C. colurna* in the Botanical Garden of Zürich had many staminate catkins forked at their tips. In *C. avellana*, 20-30 staminate catkins form very dense clusters sometimes (PENZIG 1894).

Filberts are anemophilous and nectarless just like hornbeams, birebes, alders, oaks and beaches (JONES 1939). Pollen is produced in abundance which insures pollination. Usually, staminate and pistillate flowers of the same plant do not mature at the same time, so that the plant is functionally of one sex at a time. This mechanism favours cross pollination in filberts (PHILIPSON 1948). According to ERDTMAN (1954), pollen shedding dates of the European filbert vary from December 27th in Coimbra, Portugal to April 6th in Stockholm, Sweden. Apparently the date of pollen shedding is very much influenced by weather conditions. During the first week of April, while I am writing these lines, the male catkins of all three species of *Corylus* in St. Gallen, Switzerland, are still dormant. However, a few branches brought into room temperature began shedding their pollens within two days.

Pollen grains are borne in tetrahedral quartets, each grain being commonly provided with three pores which tend to be equally spaced around the equator. The pores project along the sides of flattened grains and give rise to a triangular outline in polar view (fig. 9, A-C). The pore type of *Corylus* is designated as a club-shaped pattern by WODEHOUSE (1959) in which the exine is gradually expanded towards the pore as seen in optical sections (fig. 9, C-F). Apertures are circular or slightly elliptical. The grain surface (texture) is smooth or faintly punctuate. The ratio between polar axis and total breadth of grains (100, P/E) varies from 77,9 in *C. colurna* to 78,9 in *C. avellana* and *C. maxima*. Hence the pollen grains of all three species fall into the suboblate shape class (ERDTMAN 1952, p. 16). In optical sections, sporoderm thickness is 1,3 microns in *C. avellana*, 1,6 microns in *C. maxima* and 1,7 microns in *C. colurna* as an average of ten measurements for each case. Unfortunately, no pollen material was processed for the purpose of analysing sporoderm stratifications. The exine of *Corylus* pollen consists of two thick and three very thin layers when these grains are treated with sulphuric acid, dilute chromic or potassium hydrate (WODEHOUSE 1959). PLA DALMAU (1961, p. 209) reports the exine thickness in pollen grains of *C. avellana* as between 0,5 and 0,7 microns.

I surveyed 200 pollen grains of each species to find out the frequencies of pore numbers in each species. Dimensions of pollen grains summarized in Table III are based on 25 measurements in each case. The first figures
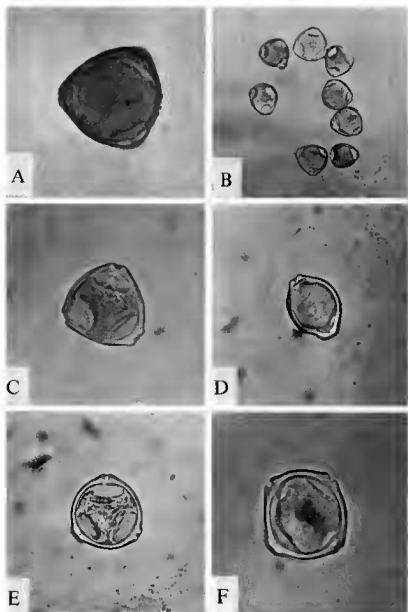
Fig. 9. — **A–F**, Photomicrographs showing the optical sections of pollen grains : **A**, Polar view of a pollen grain of *C. avellana* stained with methylene blue, 1200 ×; **B**, Pollen grains of *C. maxima*, bleached, but unstained, 460 ×; **C**, Polar view of a pollen grain of *C. maxima*, 1000 ×; **D**, Equatorial view of a pollen grain of *C. maxima*, unstained, 1000 ×; **E**, Polar view of a 3-porate pollen grain of *C. colurna*, unstained, 1000 ×; **F**, Polar view of a 4-porate pollen grain of *C. colurna*, unstained, 1200 ×.

TABLE III. — COMPARISON OF THE PALYNOLOGICAL CHARACTERISTICS
AND DIMENSIONS OF POLLEN GRAINS IN THREE SPECIES OF *Corylus*.

FEATURES	*Corylus avellana*	*Corylus maxima*	*Corylus colurna*
Source of material	Breslau (C. Bæniz, Herb. Paris)	Pisa (Cesati n° 750, Herb. Paris)	Kastamoni, Tosya, Gavurdagh (Sintenis no. 4809, Herb. Paris)
Number of pores..	All 3-porate	Mostly 3-porate, rarely 2-or4-porate	Mostly 3- or 4- porate, rarely 2-5- and 6- porate.
Texture	Psilate-faintly punctuate	Same	Same
Shape classes.....	Suboblate 100. P/E = 78.9	Suboblate 100. P/E = 78.9	Suboblate, 100. P/E = 77.9
Equatorial diameter as seen at polar view...	25,2 (23.2-27.2)	24.7 (22.4-27.2)	25.9 (12.8-30.7)
Polar axis........	19,9 (19.2-21.6)	19.5 (17.6-20.8)	20.2 (17.6-24.0)
Thickness of aspis (protrusion of germ pore)	2.2 (2.0-2.5)	2.9 (2.8-3.2)	3.0 (2.8-3.2)
Thickness of sporoderm	1.3 (1.2-1.6)	1.6 (1.5-1.8)	1.7 (1.6-1.9)
Diameter of aperture	2.0 (1.8-2.4)	2.0 (1.6-2.4)	1.7 (1.2-2.4)

given for each item represent the average values in microns. The extreme values, i. e. minimum and maximum dimensions are indicated in parentheses following the average values.

In the material I examined, the pollen grains of *C. avellana* were exclusively 3-porate. However, ERDTMAN (1954, referring to SANDEGREN's data) reports that out of 2 000 grains 99,8 % had three and 0,2 % two or four pores. In the literature, the equatorial diameter and the polar axis length given for pollen grains of *C. avellana* differ considerably. Average dimension with respect to equatorial diameter and polar axis is 25,2 × 19,9 microns in my survey. Pollen dimensions of *C. avellana* are variously reported in literature: 28 × 22 (ERDTMAN 1954), 26.5 × 22 (WODEHOUSE 1959), and 25 × 22 microns (PLA DALMAU 1961). Dimension extremes given by HEGI (1957) vary from 22-32 microns for the equatorial diameter and from 15 -18 microns for the polar axis as contras-

ted to my figures of 23,2-27,2 and 19,2-21,6 microns respectively. These differences in pollen dimensions may be attributed either to a racial difference within the same species or to different methods of treatment during the preparation of pollen slides. As a matter of fact, SCHOCH-BODMER (1936), FAEGRI and DEUSE (1960) and DRUGG (1962) demonstrated the variations in dimensions of pollen grains according to mounting media and preparation techniques.

Pollen grains of *C. maxima* are more similar to the grains of *C. avellana* than they are to those of *C. colurna*. 99 % of the grains of *C. maxima* are 3-porate and 1 % only 2- and 4-porate. Average dimension of 3-porate grains is 24,7 × 19,5 microns. The dimension of 2-porate grains is 25,6 × 20,8, of 4-porate grains 24,8 × 20,8 microns. Sporoderm is thicker than that of *C. avellana*, but the diameter of aperture is nearly the same as in *C. avellana*.

Pollen grains of *C. colurna* show more striking variation than those of the other two species. 68,5 % out of 200 grains are 3-porate, 29 % four-porate, 1 % two-porate, 1 % five-porate and 0,5 % six-porate. The equatorial diameter of 2-porate grains measures 14,4 (12,8-16,0 microns; their outline somewhat resembles the equatorial view of a regular 3-porate grain. Most likely, these grains are sterile. Three-porate grains have an equatorial diameter of 26,0 (20,8-28,8) microns; their outline tends to be somewhat circular rather than being triangular in polar view (fig. 9, E). Due to pronounced protrusion of germ pores. 4-porate grains ordinarily appear somewhat like a square in polar view (fig. 9, F). The longest equatorial axis of 4-porate grains measures 27,1 (25,6-30,7) microns between two opposite apertures. Occasionally, 4-porate grains appear in rectangular outline in polar view. Such grains are much smaller than the majority of 4-porate grains, measuring 12,5-14 microns along the short edge of the rectangle and 11-17 microns along the long edge, as seen in polar view. The equatorial diameter of 5-porate grains is 22,0 (21,6-22,4) microns; their outline in polar view is pentagonal. Apparently 6-porate grains are very rare. The only such grain which was observed had an equatorial diameter of 22,4 microns, the grain outline being hexagonal. 7-porate grains have not been observed. The mean dimensions of all five different types of pollen grains in *C. colurna* are presented in Table III.

It is interesting to note that the dimensions of any particular structure of pollen grains, including the thickness of aspis and sporoderm, exhibit as wide a range of variation as any other structure which has been considered in the present study.

PISTILLATE FLOWERS AND FRUITS

The inflorescences bearing pistillate flowers are quite different from staminate catkins. Pistillate flowers are borne in mixed buds which develop in leaf axils or lateral to terminal buds. At an early stage, from

late summer through winter, mixed buds are externally quite similar to purely vegetative buds. In addition to young folded leaves and their stipules, they contain also 4-8 pairs of pistillate flowers at their tips. Mixed buds remain dormant until early spring. Only crimson coloured stigmas of pistillate flowers protrude from bud scales at the time of pollination. During dormancy, mixed buds are 5-6 mm. long in *C. avellana* and *C. maxima*, 7-8 mm. long in *C. colurna*. About 8-9 oval and concave bud scales with ciliate margins and chaffy flaps envelope primordial leaves and pistillate flowers. Bud scales are tomentous on their abaxial sides and glabrous on the adaxial surfaces, except at their bases where unicellular trichomes are crowded. Eventually, mixed buds develop into short, leafy branches which at their tips carry the cluster of fruits.

Pistillate flowers form dichasial cymes in the axils of subtending bracts which are helically arranged around the condensed axis of mixed buds. Ordinarily, in cymules the central flower is absent. Until pollination, each flower consists of two long stigmas and a bulbous base halfway covered by primordial prophylls which upon maturity develop into fruit involucra (husk). Pistillate flowers of *C. avellana* and *C. maxima* dissected about the middle of October had stigmas from 1800 to 2600 microns long and from 140 to 220 microns thick. At this stage, the "bulbous" base measured 580 microns in diameter. The primordial calyx was hidden inside the primordial involucra. Ovary and ovules develop from an intercalary meristem at the stigma base during May (HAGERUP 1942). Pistillate flowers of *C. colurna* dissected also around the middle of October had stigmas from 900-1000 microns long and 240-280 microns thick. Likewise, the "bulbous" base of young gynoecium which develops into an ovary after pollination, was surrounded only basally by primordial prophylls. The stigmatic surface is puberulent. The vesicle-like epidermal cells contain anthocyanine responsible for the showy purple-crimson color of the stigmas.

The bicarpellate nature of the ovary is clearly established (HAGERUP 1942, EAMES 1961) although it was formerly described as being monocarpellate. The unilocular ovary possesses two parietal placentae, each bearing 1-2 ovules. Young ovules are orthotropous and pendant, but they bend later, acquiring a campylotropous condition. The ovules have single integument, the micropyle facing upward. Chalazogamy which was discovered first by NAVASHIN, takes place in July, after 3-4 months following pollination. Usually one ovule develops into a seed while the other one becomes abortive.

For the sake of convenience, the rudimentary and undifferentiated floral envelope adnate to the ovary are referred to as "calyx". EICHLER (1878) applied the term "perigon" to it, stating that it consists of 4-8 minute teeth near the apex of the ovary. These teeth are shown as individual perianth segments in EICHLER's floral diagram for *C. avellana*. According to EICHLER, the rudimentary "perigonium" is completely obliterated during later growth. On the other hand, HAGERUP

(1942) who uses the term "perianth", shows clearly that it remains adnate to the mature fruit. So far as I know, the morphological nature of "calyx" in pistillate flowers is not known clearly. Does it originate from the intercalary meristem at the base of stigmas or is it produced by the apical meristem of the flower? Do the marginal teeth really represent perianth segments, as assumed by EICHLER? If this would be the case, a "synsepalous" condition would enter the picture. Both, vascular anatomy and histogenesis of pistillate flower of *Corylus* deserve careful investigation which may produce an answer to these questions.

The familiar nuts of *C. avellana* are 1-2 cm. long, 9-16 mm. broad and occur in clusters of 2-8 or sometimes singly. Involucral bracts are almost separate, broadly lobed, exposing the nuts. Involucral scars in the bottom of nuts are usually submedian. However, all these features are variable. GEITLER (1943) showed variation in fruit dimensions as well as in sizes and divisions of the involucral bracts in wild populations of the European filbert.

The nuts of *C. maxima* are 1,5-2,5 cm. long, 12-16 mm. broad and almost cylindrical in shape. They occur in clusters of 4-8 fruits. Coalescent involucral bracts enclose the nut within and extend beyond it. The husk splits laterally to release the nut at maturity. The involucral scar remaining in the bottom of the fruit is usually basal, but submedian scars are not uncommon.

The fruits of *C. colurna* are 15-21 mm. long, 10-18 mm. broad and ovate to obovate in shape. Usually, the nuts occur in clusters of 2-6 fruits, but larger clusters with many more fruits are also found. The nut shell in this species is much thicker, the seed within smaller than those of the other two species. In the european varieties, the involucral bracts fork deeply into lanceolate or triangular lobes, exposing the nuts half way. The husk of the asiatic varieties however, encloses the nut and even extends beyond it. Typically, the involucral scars left on the nuts are median, but this feature as well as the shape and dimensions of the nuts are quite variable (cf. KASAPLIGIL 1963 *b*, fig. 4).

Interesting teratological pistillate cymules were described by WEISS (1932). According to this author, *Corylus* shrubs pruned in hedging produce unbranched shoots which give rise to terminal pistillate cymules with three flowers. The subtending bract of such an abnormal cymule with median flower is tripartite instead of being simple. I have seen a perfectly normal staminate flower in a pistillate inflorescence of *C. maxima*. The nuts of this species are occasionally triangular, suggesting a tricarpellate fruit. Likewise, the fruits of *C. colurna* sometimes bear three wilted stigmas on top instead of the normal two (KASAPLIGIL 1963 *b*, fig. 5, K-L). EICHLER (1878, p. 17, footnote) points out that the occurrence of 2 or 3 seeds in common hazelnuts is not seldom. PENZIG (1894) reports the frequent occurrence of tricotyledonous embryos in *C. avellana*.

DISCUSSION

The present study has been dealing primarily with the histology of certain vegetative organs of three species of *Corylus* in an attempt to understand the degree of phylogenetic relationship between the species under consideration and the position of the genus within the family *Betulaceae*.

Histology has long provided taxonomy with characteristics of phylogenetic importance through comparative observations on wood anatomy, epidermal features, nodal anatomy, foliar vasculation etc. as well as through ontogenetic studies. A comprehensive review by Constance (1955) clearly shows the increasing attention of botanists in the application of histologic criteria to the problems of systematic botany. Due to convergences and parallel evolution, phylogenetic affinities can not be judged by a single line of evidence from any particular organ by using the tools of a single discipline. It is essential to survey all plant structures in the light of all disciplines in order to reach a sound natural classification (Bailey 1949). Bearing this in mind, I tried to gather some phytogeographic data and bring out additional evidences through comparative morphology and palynology. Therefore, the distribution of three species of *Corylus*, comparative morphology of their flowers and palynological characteristics have necessarily been taken into consideration.

The observations regarding vegetative and reproductive structures of three species of *Corylus* indicate close similarity between *C. avellana* and *C. maxima*, while *C. colurna* differs strikingly from the other two species. The present distribution areas of *C. avellana* and *C. maxima* coincide with each other from south-eastern Europe through northern Anatolia to the Caucasian region. The latter species has a rather restricted area while the former species presents an extensive distribution throughout Europe and in the Near East, reaching the Scandinavian peninsula in the North and the Lebanese mountains in the South. The specimens of *C. maxima* collected from north-eastern Anatolia show the widest range of variation which suggests that the center of speciation may be in this particular region of Turkey.

C. colurna with its arboreal habit remarkably differs from the other two shrubby species with respect to its anatomic structures as well as its distribution. The Turkish filbert with its four varieties grows from south-eastern Europe through northern Turkey and the Himalayas up to China. Only the western tip of its area overlaps with the distribution areas of the other two european species. I assume that *C. colurna* is more closely allied with *C. ferox* Wall. = Himalayan filbert, than it is either with *C. avellana* or *C. maxima*. The areas of *C. colurna* and *C. ferox* coincide with each other in the Himalayan region. Both of these arboreal species might have been derived from a common arboreal ancestor. The involucral bracts around the nuts of *C. ferox* are highly lignified

and very spiny, the whole cluster of fruits resembling a chestnut bur. However, a close examination reveals the fact that the involucral bracts in *C. colurna* and *C. ferox* are deeply laciniate, the slender lobes being stiffly spinose in the latter species and sinuous in the former. Unfortunately, there is no information on the finer structure of *C. ferox* to make a further detailed comparison with *C. colurna*. Considering their distribution and gross-morphological features, *C. colurna* var. *lacera* (Wall.) A. DC. stands nearest to *C. ferox*, as far as I can judge.

Primary stem structure is basically the same in all three species studied. Solitary crystals and druses of calcium oxalate occur in the cortex, phloem and pith tissues of stems as well as in the foliage leaves and floral bracts, a feature which is also common in other betulaceous genera such as *Alnus, Betula, Carpinus, Ostrya*. In three year old stems of *C. colurna*, druses occurring in cortical parenchyma, secondary phloem and pith parenchyma are considerably larger than those of the other two species. This seems to be a good diagnostic feature for *C. colurna*. The size variation of druses within the tissues mentioned above, particularly those in cortical parenchyma, show a narrow range in *C. avellana* and *C. maxima*, a wider one in *C. colurna*. The frequencies of size classes of druses follow a similar pattern (fig. 1, A-C) in *C. avellana* and *C. maxima* which may be considered as an indication of closer affinity between these two species.

In *C. colurna*, the cortical collenchyma of three year old stems is a continuous cylinder while in *C. avellana* and *C. maxima* it is interrupted by the secondary stem growth. Bizarre brachysclereids occur individually or in clusters within the secondary phloem tissue of *C. colurna* stems, while these idioblasts are absent or exceedingly rare within the corresponding tissue of the other two species. The restitutional capacity of the cortical collenchyma and the extensive occurrence of brachysclereids in *C. colurna* stems may be looked upon as a more specialized condition.

The wood of *Corylus* and of all other genera of *Betulaceae* is diffuse porous, the pores being arranged radially as seen in cross sections. Waviness of growth layers in secondary xylem is a common characteristic for *Corylus* as well as for other genera of *Betulaceae*, except for certain species of *Betula*. The undulations of growth layers are most prominent in the species of *Carpinus* and hardly noticeable in *Betula pendula* and *B. pubescens*. However, *Betula humilis, B. nana* and *B. raddeana* stems exhibit clear undulations of growth layers in transverse sections (GREGUSS 1959, pl. 2, 3, and 6). The number of xylem rays varies from 16 rays per millimetre in *C. colurna* to 22 rays per millimetre in *C. maxima*. In species of *Alnus* and *Betula*, the number of xylem rays per millimeter varies from 16 to 20 and from 14 to 22 respectively. Minor differences aside, the numerical ranges of xylem rays mentioned above are fairly close to each other in these genera.

The vessel members bear scalariform perforation plates throughout the family. The perforation plates in *C. avellana* and *C. maxima* are wider, the number of bars is smaller than in *C. colurna* which suggests a more

specialized condition in the first two species. On the other hand, the vessel members of *C. colurna* are much shorter than those of the other species. There is a peculiar combination of advanced and primitive features in these elements. The number of bars in scalariform perforation plates varies from 10 to 20 in the species of *Betula* and from 10-22 in the species of *Alnus* (cf. GREGUSS 1959, pls. 2-10). This variation falls within the range of variation observed in the perforation plates of *C. colurna*. (Furthermore, pointed end walls of vessel members and the obliqueness of perforation plates seem to be a common feature throughout the family.) Bifurcation of perforation bars described in *C. maxima* and *C. colurna* also occurs in *Alnus subcordata*, *A. viridis*, *Betula humilis* and *B. nana*. Pointed end walls, oblique perforation plates and the main features of pitting seem to be more or less uniform throughout the family despite certain variations. Tertiary helical thickenings described for vessel elements of *Corylus* occur also in *Betula raddeana*. According to HALL (1952), helical thickenings are present in the vessels of *Carpinus*, *Ostrya* and *Ostryopsis*.

Tracheids and vessel members constitute the bulk of the secondary xylem in *C. colurna* while in *C. avellana* and *C. maxima* the bulk of wood consists of fiber tracheids. Tracheids are tapering cells with pointed tips bearing many rounded or elliptical bordered pits. This characteristic applies to the whole family. Tracheids and all other vertical wood elements are generally shorter in *C. colurna* than in the other two species. The occurrence of brachysclereids in xylem rays seems to be a specialized condition limited to *C. colurna*. Aggregate xylem rays occur throughout the family, although infrequently. Likewise, apotracheal diffuse parenchyma with a tendency to metatracheal and paratracheal conditions is a common characteristic of most of the genera in the family. The supplementary fibers (Ersatzfasern) observed in wood parenchyma of *C. colurna* represent another distinguishing feature.

In *Corylus* as well as in other genera of the family, leaves are simple, stipulate and arranged alternately. With the exception of entire-leaved *Alnus nepalensis*, leaf margins are doubly serrate. In *Corylus*, very young leaves enclosed within buds are folded along midribs. This feature constitutes a generic characteristic for *Corylus* since the young leaves within buds are folded along secondary veins in all other genera of the family. Unicellular simple trichomes are common throughout the family, but septate simple trichomes described for *Corylus* occur in *Alnus* and *Ostrya* as well. Capitate-glandular trichomes occur frequently in the family. The stalk of the capitate-glandular trichomes in *Carpinus betulus*, *C. caroliniana*, *Ostrya carpinifolia* and *O. virginiana* (cf. METCALFE and CHALK 1957, vol. 2, p. 1302, fig. 311, G-H) consists of a single row of cells which seem to be a modification of capitate-glandular trichomes described in *Corylus*. With respect to the form of their glandular heads, these trichomes stand intermediate between typically capitate hairs and club-shaped glandular hairs of *Corylus* (Fig. 3, D and H). Peltate glands or scales bearing a palisade like glandular epidermis in *Betula*

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(ESAU 1953, p. 156, fig. 7, 10, E; HEGI 1957, 111/1, p. 142, fig. 55, e; METCALFE and CHALK 1957, II, p. 1302, fig. 311, B-D) and *Alnus* simply represent a modification of capitate glandular trichomes of *Corylus* (cf. fig. 3, A-D). The somewhat flattened head of glandular trichomes of *Ostrya* seems to represent an intermediate form between capitate-glandular trichomes of *Corylus* and peltate scales of *Betula* and *Alnus*. Radiating secretory cells seen in fig. 3, A-D, are very similar indeed to the palisade-like glandular epidermis of peltate scales. The multi-cellular stalks of these trichomes are obviously similar to those of the glandular trichomes except for the fact that the stalks of peltate glands are shorter and that they are somewhat sunken in the leaf surface. The glandular emergences described here (fig. 3 G) do not occur in other genera. They seem to represent a generic characteristic for *Corylus*.

In agreement with METCALFE and CHALK (1957) the stomata definitely have subsidiary cells, although some recent literature (HEGI 1957, 111/1, p. 138) claims that they are absent. The anomocytic stomata in *Corylus* as well as in other members of *Betulaceae* are confined to the abaxial leaf surfaces (except in *Alnus orientalis* which has stomata on both sides). However, this feature may not be of phylogenetic significance since many unrelated angiosperms possess anomocytic stomata. Both, upper and lower epidermises of juvenile leaves of all three species of *Corylus* exhibit undulations along the anticlinal cell walls while the undulated epidermal cells are confined only to the lower surfaces of adult leaves. A similar condition in the juvenile leaves of *Umbellularia* and *Laurus* was interpreted by the author as a seedling recapitulation (KASA-PLIGIL 1951, p. 161-164). The abaxial epidermis of adult leaves in *C. colurna* tends to develop stellate epidermal cells, a specialized condition not observed in other species of *Corylus*. Mucilaginous cells in epidermis occur widely throughout the family.

Craspedodromous type of major venation pattern of leaves is a common feature in all members of the family. In the different genera, secondary veins are straight or slightly curved. Their divergence angles from the midrib vary between 50-60° in *Alnus*, 45-75° in *Betula*, 35-45° in *Carpinus* and 40-50° in *Ostrya* (ETTINGSHAUSEN 1861). In *Corylus* leaves, the divergence angles of the secondaries show a wider range of variation due to the auriculate condition of the cordate basis of blades and the abrupt acuminate form of the leaf apices. In the genera mentioned above, the tertiary veins develop from the basiscopic sides of the secondaries and terminate in marginal teeth (cf. ETTINGSHAUSEN 1861, Pl. 1, fig. 5 and Pl. II, fig. 1, 4, 10, 11). This holds true also for *Corylus*. Another striking resemblance concerning major venation is the fact that the number of tertiaries diminishes gradually towards the leaf apex.

The minor venation of juvenile leaves of *Corylus* consists of veins of fourth, fifth and sixth categories and of vein endings. In the adult leaves, an additional category of minor veins is present. Apparently, veins of the seventh category are derived from further ramification of

veins of the sixth category. Their frequent anastomoses result in the formation of ultimate areoles and in a complex reticulum in adult leaves. Possibly, the evolution of the venation pattern in *Corylus* follows a trend from a simpler reticulum towards a more complex venation pattern. Most of the ultimate areoles in adult leaves of *C. colurna* are provided with slender and repeatedly branched vein endings, which under a hand lens, help to distinguish *C. colurna* leaves from the leaves of other species.

In *Corylus*, the main vascular bundle of petioles at the level of the "coupe caractéristique" appears closed elliptical or reniform in outline, but often they shift to crescent shape in the midrib of leaves. METCALFE and CHALK (1957) report crescentic vascular strands in the petioles of *Alnus* and *Betula* which seem to be similar to the outline of some main vascular strands in the midribs of *Corylus* leaves. SOLEREDER (1908) reports that in *Alnus* and *Betula*, three or more bundles enter the petiole base, a condition which supports my assumption that the tripartite vascular bundle in *Corylus* resulted from the fusion of the originally separate three bundles.

Generally, it is considered, that the staminate flowers of *Corylus* consist of "divided stamens". As I explained in the text, I found no evidence of "divided stamens" in the material I studied. If we accept the claims regarding complete division of stamens all the way down to the base of filaments, we would expect to find even number of "half stamens" instead of odd numbers. The fluctuation of the number of stamens per flower was pointed out earlier in this paper. Flowers with 5, 7, 9 stamens are not uncommon. One would immediately suspect the abortion of a "half stamen" from a "normal flower" with an even number of stamens, but there is no sign of abortive stamens in flowers with an odd number of stamens.

According to EAMES (1961, p. 132) the single vascular bundle of the stamen arises from two traces in *Corylus*. I interpret this condition as the fusion of two traces giving rise to the vascular supply of a stamen. Hence, even the vascular anatomy of the stamen does not seem to be in agreement with the assumption of divided stamen in *Corylus*. However, before knowing the ontogeny of stamen in *Corylus*, it is not possible to make a clear-cut decision at this point.

Pollen grains of *Corylus* are mostly 3-porate, but this number is not well established in the species I studied. The pore number fluctuates from 2 to 4 in *C. avellana* and *C. maxima*. However 2- or 4-porate grains are very rare in both species. On the other hand, 4-porate grains show a high frequency in *C. colurna*. Grains with 2, 5 and 6 pores also occurred in a pollen crop obtained from a single catkin. Different pore numbers of grains does not appear to be a racial characteristic. Perhaps, these differences are caused by chromosomal non-disjunction and aberration which often take place in *C. colurna* during meiosis of microsporogenesis. Pollen grains with different pores occur in several other genera of *Betulaceae*. Pollen grains of *Alnus* are often 4- to 5-porate, rarely 3- or 6-porate

(WODEHOUSE 1959). Particularly, 4-porate grains of *A. glutinosa* (ERDT-MAN 1954, p. 68, Pl. IV, fig. 52-53) and *A. incana* (*ibid.*, Pl. IV, fig. 56-57) are very similar to the 4-porate grains of *C. colurna*, but the pollen grains of *Alnus* differ from filbert pollen, mainly through the presence of an endexinous floor under each pore. Pollen grains of *Betula* are mostly 3-porate, but grains with 4 to 7 pores also occur (WODEHOUSE 1957). The pores of *Betula* pollen project more strikingly than those of *Corylus* pollen. FIRBAS, F. and I. (1958) report that the pollen grain of *Carpinus betulus* fluctuates between 2- and 7-porate conditions, 4-porate grains being most frequent. These authors also point out the variation of pore numbers in grains from a single catkin and attribute the possible cause of it to differences in the nutrient supply required for the formation of pollen grains. The pores of pollen grains of *Betula* are more strikingly aspidate than those of *Corylus*. Pollen grains of *Ostrya* are either 3- or 4-porate. Apparently, *Ostryopsis* is the only genus which exhibits a fixed 3-porate condition only (ERDTMAN 1952). As a whole, mean size variation of pollen grains in the family ranges from 20 to 30 microns according to ERDTMAN (1952). They all exhibit a suboblate shape and psilate or faintly punctuate texture. In short, pollen grains of *Betulaceae* are rather homogeneous, an indication of close affinity among the genera of the family.

The pistillate flower of *Corylus*, as I pointed out earlier in this paper presents a number of problems. Perhaps, one of the most important questions concerns the position of the ovary which by several authors has been considered as being inferior. This "criterium" has been used hastily to segregate Corylaceae from Betulaceae. Is the ovary in *Corylus* really inferior? Indeed, the so-called "calyx" or "perigonium" is adnate to the ovary. As I explained before, we do not know the true morphological nature of the "calyx" in *Corylus*. It may be an appendicular or receptacular structure; both instances would justify designating the ovary as being inferior. On the other hand, the "calyx" of *Corylus* may represent modified bracteoles or even non-functional gynoecial nectaries. In such instances, however, the ovary can not be considered inferior. The solution of this morphological puzzle awaits further investigation, particularly from the viewpoints of histogenesis and vascular anatomy.

Considering the phylogenetic trends in gynoecia of Angiosperms (CONSTANCE 1955, p. 427) the bicarpellate, syncarpous gynoecium of *Corylus* with a reduced number of ovules is highly evolved. The occasional occurrence of tricarpellate fruits in *Corylus* may be considered a reversion, i.e. possibly the bicarpellate gynoecium of *Corylus* is derived from a tricarpellate gynoecium through the reduction of one of the carpels. Likewise, the ovules show a reduction from four to two and finally only one seed develops per fruit, the other ovule remaining abortive.

It is not easy to interpret plant teratologies although there is a general tendency to speculate about structural aberrations as being genetic reversions or so-called "atavisms". In accordance with such a speculation, teratologically hermaphroditic flowers of *Corylus* described by HJELMQVIST (1948) may be interpreted as being a prototype for the present

unisexual flowers. The pistillate cymules of *Corylus*, *Alnus* and *Carpinus* normally consist of two flowers. The occurrence of a third flower was reported by Weiss (1932) in *Corylus*, by Kirchner, Loew and Schröter (1913, p. 196) in *Alnus* and by Hegi (1957 III/1, p. 182) in *Carpinus*, a situation very similar to normal cymules of *Betula*.

Undoubtedly, *Corylus* is a homogeneous genus. Nevertheless, the degree of genetic affinity among the member species varies. From my present survey on three species, I conclude that *C. avellana* and *C. maxima* are two closely allied species and *C. colurna*, which exhibits distinct structural and distributional deviations from both other species is a distant relative. Several hybrid forms between *C. avellana* and *C. maxima* are well known cultivated plants. These hybrids produce nuts which is an evidence of interfertility and close genetic relationship between these two species. On the other hand, the hybridization between *C. colurna* and either one of the other two species does not seem to be possible. The hybrid species *Corylus* × *colurnoides* Schneid. (Syn. : *C. avellana* × *colurna* Rehder, *C. colurnoides* Schneid., *C. intermedia* Lodd.) described from cultivated plants, is not known from natural populations although the areas of supposed parents overlap each other in south-eastern Europe and in the Near East. No specimen of the well known "hybrid species" exists in any of the following herbaria: Univ. of California, Berkeley; Royal Botanic Gardens, Kew; Muséum d'Histoire Naturelle, Paris; Conservatoire Botanique, Geneva; Botanisches Institut, Zürich; Naturhistorisches Museum, Vienna. Moreover, *C. colurna*, although always cultivated in the vicinity of either one of the other two species in Europe, produces sterile fruits only unless a heterogenic population of *C. colurna* grows in the vicinity (Kasapligil 1963 a, b). The existence of *C. colurnoides* as a hybrid species is most doubtful.

Considering the histologic, palynologic and morphologic evidences presented here, *Betulaceae* which comprises *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Ostrya* and *Ostryopsis* represents a natural group. The segregation of *Corylaceae* from *Betulaceae* is not justified.

St. Gallen, Switzerland, Apr. 11, 1963.

SUMMARY

The present study deals with the histology of the vegetative organs and the floral morphology of three European species of *Corylus* in an attempt to understand the degree of phylogenetic relationship among the species under consideration and the taxonomic status of the genus within the family *Betulaceae*.

The collenchyma in the stems of *Corylus avellana* and *C. maxima* becomes interrupted, the gaps being occupied by thin-walled parenchyma cells. In *Corylus colurna*, collenchyma of stems remains as a continuous cylinder due to the restitutional capacity of its cells.

The average sizes and the frequencies of the size classes of calcium

oxalate druses in the stem tissues of *C. avellana* and *C. maxima* are quite similar, but the druses in different stem tissues of *C. colurna* are larger than those of the corresponding tissues of *C. avellana* and *C. maxima*. Particularly, the frequencies of the size classes of cortical druses in *C. colurna* deviate considerably from those of the other two species, a fact bearing diagnostic significance for *C. colurna*.

The bulk of the secondary xylem consists of relatively thin-walled, imperforate tracheary elements in *C. avellana* and *C. maxima* and of vessel elements and thick-walled tracheids in *C. colurna*. Due to the presence of aggregate rays, the growth layers are more or less wavy. There are 21 xylem rays per millimetre of stem section in *C. avellana* and *C. maxima*, but in *C. colurna* the corresponding number is 16. The latter species differs considerably from the other two by the presence of brachysclereids in the secondary xylem rays.

The species under consideration show the following types of trichomes : unicellular simple, septate simple, tufted, capitate glandular, club-shaped glandular and conical glandular. The structural relation between these trichomes and those occurring in other betulaceous genera is pointed out. Glandular emergences are confined to *Corylus* and constitude a generic character.

Juvenile leaves from the seedlings of *C. avellana* and *C. maxima* and those from the sucker-shoots of *C. colurna* are characterized by the presence of undulate epidermal cells on both abaxial and adaxial sides, while the adult leaves of all three species possess undulate epidermis on the lower side and rectangular or polygonal cells on the upper side. The abaxial epidermis of adult leaves of *C. colurna* shows a tendency to form stellate cells. The stomata are of anomocytic type and confined to the lower epidermis, the number of subsidiary cells varying from four to six.

Major venation of juvenile and adult leaves is of craspedodromous type and consists of primary, secondary and tertiary veins, all of which are accompanied by bundle sheath extensions. The secondaries form a pinnate venation pattern and terminate in marginal lobes. The tertiaries arise from the basiscopic sides of the secondaries and terminate in marginal teeth. The number of tertiaries diminishes gradually towards the leaf apex. Throughout the family, the major venation pattern is uniform. Minor venation of the juvenile leaves consists of veins of fourth, fifth, sixth categories and vein endings, while the minor venation of the adult leaves possesses an additional category of veins forming a more complex reticulum in adult leaves. Ultimate areoles in the adult leaves of *C. avellana* and *C. maxima* are polygonal; they may or may not be provided with vein endings. Ultimate areoles of *C. colurna* are often rounded and provided with slender and repeatedly branched vein endings.

The collenchyma tissue of petioles is capable of regeneration and gives rise to periderm, following the secondary growth of the main vascular bundle of the petiole. At the level of "coupe caractéristique", the main vascular bundle of the petiole is tripartite and accompanied by an arch-shaped accessory bundle in *C. avellana*. On the other hand, in

C. maxima and *C. colurna* the main vascular bundle at the same level of the petiole exhibits a more specialized condition since the tripartite condition is no longer evident and the accessory bundle is closed-cylindrical.

Gross morphological survey of the staminate flowers did not furnish any evidence in favor of "divided nature" of stamens in *Corylus*. Pollen grains are suboblate, the texture of the exine being psilate to faintly punctuate. Those of *C. avellana* surveyed in this study are 3-porate, their dimension being 25,2 × 19,9 microns. Pollen grains of *C. maxima* are mostly 3-porate, rarely 2- or 4-porate, their dimension being 24,7×19,5 microns. *C. colurna* has mostly 3- or 4-porate grains, less frequently 2-, 5- and 6-porate grains, mean dimensions being 25,9 × 20,2 microns. Variation in the pore numbers of the pollen grains does not appear to be a racial characteristic. Great variation in the pore number of the pollen grains is attributed to chromosomal aberrations and non-disjunctions which take place quite often during meiosis of microsporogenesis. Palynological evidence favours the homogeneity of *Betulaceae*.

The observations regarding vegetative and reproductive structures of three species of *Corylus* indicate close affinity between *C. avellana* and *C. maxima*. It is assumed that *C. colurna* is more closely allied with *C. ferox* than it is either with *C. avellana* or *C. maxima*. Hence, the possibility of hybridization between *C. colurna* and the other two species is very unlikely. The validity of the hybrid species *Corylus* × *colurnoides* Schneider is most doubtful.

The woods of *Corylus* exhibit specialized characteristics such as aggregation of pores, the presence of aggregate rays, a tendency to form homogeneous xylem rays and a metatracheal arrangement of xylem parenchyma, the presence of a great variety of xylem elements, a reduction series in the number of bars of the scalariform perforation plates with a tendency to form simple perforation plates and alternate pitting. However, primitive characters such as diffuse porosity, polyhedral vessel elements, inclined end walls, abundance of bordered pits and scalariform perforation plates are also retained in the genus. Evidence from foliar histology, floral morphology and palynology, however, indicates that the genus occupies 'quite an' advanced position in the phylogenetic scale of dicotyledons. *Betulaceae* with its six genera, is considered a natural family. The segregation of *Corylaceae* from *Betulaceae* is not justified.

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